AMAZONIANA	IV	1	9 – 102	Kiel, März 1973

(From: Cooperation between Max-Planck-Institut für Limnologie, Abt. Tropenökologie, Plön, Germany, and Instituto Nacional de Pesquisas da Amazônia, Manaus-Amazonas, Brazil)

Investigations on the Ecology and Production-Biology of the "Floating Meadows" (Paspalo-Echinochloetum) on the Middle Amazon[1]

Part II. The Aquatic Fauna in the Root Zone of Floating Vegetation

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[1] Brazilian Contribution of the International Biological Programme, Section PFM; Contribuição brasileira ao Programa Biológico Internacional, Secção PFM.

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I. Introduction

Multitudes of floating plants occur in the Amazon itself, as well as in its floodplain, the várzea. *Paspalum repens* BERG and *Echinochloa polystachya* (H.B.K.) HITCHKOCK (Family Gramineae) are especially important. These are well adapted to the ecological conditions of this region, particularly the wide fluctuations in water level. During the high-water period they form the characteristic 'floating meadows' of the várzea region, which extend over many square kilometers (JUNK 1970). SIOLI (1965) has pointed out the richness of the aquatic fauna in the floating masses of plants, and MARLIER (1965) has given the first biomass data for the invertebrates in them.

The pursuit of a more comprehensive knowledge of the animals in these vast expanses is stimulated by observations of others (BRAUN 1952, MARLIER 1965) that temporarily benthic animals are sparse in the lakes. Moreover, SCHMIDT (1972) reports that extensive oxygen depletion, and even H_2S formation, often occur near the bottom of várzea lakes during highwater, so that fauna are excluded from large portions of the benthic habitat, at least temporarily. Floating vegetation must therefore be considered an important site for primary, as well as secondary, production in the várzea region.
The goals of the present investigation were to increase knowledge of the aquatic fauna in floating vegetation, to evaluate their biomass and to elucidate the more important ecological factors which affect the biocoenoses.

II. The floating vegetation as biotope for the aquatic fauna

Floating vegetation represents a very special habitat for faunal settlement. The most significant feature, no doubt, is that an aquatic biotope in the root zone and a more terrestrial one among the leaves and flowers occur side-by-side, and are connected to each other by a very extensive, continuously transitional zone. In consequence, the 'floating meadows' are inhabited by a combination of aquatic, semi-aquatic and terrestrial forms[1].

That parts of the floating meadows, which extend above the water's surface naturally serve as habitats for many of the insects whose larvae inhabit the aquatic zones, e.g., Chironomidae, Ceratopogonidae, Trichoptera, Ephemeroptera, Odonata etc.. Other colonizers include those forms which can swim or move about to some extent on the surface of the water, and those which parasitize the plants (BENNETT and ZWOELFER 1968). To these groups belong, among others, various Collembola, Arachnida, Pyrolidae, Blattidae, Curculionidae etc.. Still others are obligate terrestrial forms. In periods of low water levels, the stranded margins of the meadows are rapidly invaded from land by a variety of terrestrial species. As the water

[1] Our quantitative studies included only the aquatic animals; however, for the sake of completeness, several ecological observations on the remainder of the fauna will be presented at the outset.

rises, these animals are cut off from shore and must retreat to the emergent portions which remain of the terrestrial vegetation. When these, too, are submerged, the animals must transfer residence to the floating vegetation or drown. The same is true for animals cast up on the meadows by the current. Thus these floating masses serve as a refuge on which fauna can more or less successfully survive through the seasonal floods. The many species of Formicidae provid an apt example: various species, including fire ants, occur in great abundance on dense hummoc or in hollow stalks. When the meadows come to rest on dry ground, these ants move directly out onto the former lake floor. Strictly terrestrial forms have greater chances for survival when floating vegetation is denser and more stable. In accordance, young *Paspalum repens* and *Echinochloa polystachya* stands in the Amazon are normally less heavily populated by land-dwellers than thicker, older mats in the lakes, which support trees and in many other respects are biotopically very similar to the banks.

Finally, there are the large numbers of waterfowl, which remain mainly on the edges of the floating vegetation during the day. Certainly, these are the most edifying residents of this biotope.

The submerged zone of the floating vegetation consists of a tight entanglement of roots and rhizomes which provide a substratum for sessile forms. In the interstices are larger or smaller spaces of open water in which pelagic forms can live. Broad fluctuations in dissolved oxygen can occur in the smaller spaces, and in older, denser stands, this can reach the point of total oxygen depletion and formation of H_2S. The aquatic zone is by no means an homogeneous environment therefore, but is subdivided into many ecological niches. The faunal diversity is correspondingly rich. Since taxonomic and faunistic investigations of this community have only begun, exact identifications were impossible in most cases. Present description must be restricted to a brief characterization of the biocoenoses.

Crustacea:

The most abundant groups within the Crustacea were Copepoda, Ostracoda, Cladocera and Conchostraca. The occurence of a species of Conchostraca - *Cyclestheria hislopi* BAIRD 1) which in South-American papers sometimes is determined as *Gatuna spinifera* - appeared to be characteristic of particular biotopes.

Mysidacea and Amphipoda were occasionally represented by single individuals. Decapoda on the other hand, were common, particularly species of the family Palaemonidae (*Macrobrachium amazonicum* HELLER and *Macrobrachium jelskii* MIERS 2). These occurred at all stations and were sometimes abundant (100 per 1/4 m^2). Examination of their digestive tracts revealed that the shrimp had fed on Chironomidae, Conchostraca etc., but had also ingested many roots. Brachyura were found only rarely.

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1) Identified by McKenzie, British Museum, London

2) Identified by H. Holthuis, Zool. Mus., Leiden

Insecta:

Several orders of insects were abundant. Diptera, especially, composed a significant fraction of both total abundance and biomass in almost every biotope.

Most individuals of this order belonged to the family Chironomidae, but Ceratopogonidae were also abundant. Single Culicinae were present and Chaoborinae were rare. Several other families were represented by a few specimens, e. g., Stratiomyidae, Tabanidae, Tipulidae, Syrphidae etc.

The presence of Odonata is readily apparent from the showy imagines; this order is mainly represented by Anisoptera. The fraction of Zygoptera was relatively larger in flowing whitewater than in lakes. Examination of the gut contents revealed a mixture of Cladocera, Conchostraca and Chironomidae which varied with the size of the predator.

Other abundantly represented orders were Coleoptera, Trichoptera and Ephemeroptera. A frequent form, especially in the lakes, was *Asthenopus spec.* 1). Scattered Lepidoptera were present, but no Plecoptera were taken.

Hemiptera regularly turned up in the samples. An inital perusal of the material yielded the following species 2):

Belostoma discretum MONTANDON (Fam. Belostomatidae)
Belostoma micantulum STAL (Fam. Belostomatidae)
Belostoma dentatum MAYR (Fam. Belostomatidae)
Ranatra parvula KUITERT (Fam. Ranatridae)
Limnocoris spec. (Fam. Naucoridae)
Ambrysus spec. (Fam. Naucoridae)
Pelocoris spec. (Fam. Naucoridae)
Neoplea spec. (Fam. Pleidae)
Tenagobia selecta (Fam. Corixidae)

In July, 1967, masses of *Tenagobia selecta* and *Tenagobia signata* converged on favorably situated light sources in Manaus, but this phenomenon did not recur in 1968.

Mollusca:

The most abundant molluscan group is the Planorbidae. *Biomphalaria straminea* DUNKER, *Biomphalaria amazonica* PARAENSE, *Drepanotrema depressissimum* MORICAND, *Drepanotreme anatinum* ORBIGNY and *Drepanotrema lucidum* PFEIFFER have been found (LOBATO PARAENSE 1967). The presence of *Biomphalaria straminea* is especially significant, as it is the intermediate host of *Schistosoma mansoni. Riophalaria straminea*

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1) Identified by G.F. Edmunds jr., University of Utah.

2) Identified by H.H. Weber, 23 Kiel.

is generally distributed among the roots of the floating vegetation. Nevertheless, with the exception of Fordlandia on the Rio Tapajós , there has so far been no known epedemic of schistosomiasis in the Amazonian basin. SIOLI (1953) attributes this to the low human population density and large volume of water, among other factors.

As population densities increase and infected persons immigrate from areas in the north where the sickness is common, it is quite possible that occassional appearances of *Schistosoma mansoni* will occur in the practically stagnant lakes. The possibility is greater where the population is in close contact with the water, as in jute cultivation.

Other abundant molluscan groups are the family Ancylidae and the genus *Ampullarius.* The latter seems to avoid locations exposed to the current, as well as dense stands of *Leersia hexandra* and *Scirpus cubensis.* Investigations of the gut contents revealed that they feed on detritus, decomposing plant tissues and roots of the floating vegetation. Sometimes some Bivalvia (*Eupera* (*Byssanodonta*) *bahiensis* SPIX, Fam. Sphaeriidae[1]) have been found.

Most of the vertebrates obtained with the methods employed were fishes. The following species can be considered especially characteristic of this biotope[2]:

Hemigrammus spec. (Fam. Characidae)
Hyphessobrycon spec. (Fam. Characidae)
Gymnotus carapo LINNÉ (Fam. Gymnotidae)
Cichlasoma severum HECKEL (Fam. Cichlidae)
Cichlasoma festivum HECKEL (Fam. Cichlidae)
Microphilypnus spec. (Fam. Eleotridae)
Symbranchus marmoratus BLOCH (Fam. Symbranchidae)

These species remain largely in the peripheral zones and sparser portions of the stands where available oxygen is greater. Only *Symbranchus marmoratus* was at all common within denser stands of *Paspalum repens.* Its ability to breathe atmospheric air and its eel-like body are exemplary adaptations to life within the dense plant masses.

The following species were also found:

Hoplias malabaricus BLOCH (Fam. Characidae)
Cheirodon spec. (Fam. Characidae)
Leporinus fasciatus BLOCH (Fam. Anostomidae)
Serrasalmus spec. (Fam. Serrasalmidae)
Mylossoma spec. (Fam. Serrasalmidae)
Pyrrhulina spec. (Fam. Lebiasinidae)
Eigenmannia spec. (Fam. Gymnotidae)
Stenopygus spec. (Fam. Gymnotidae)
Anadoras spec. (Fam. Loricariidae)
Hoplosternum spec. (Fam. Callichthyidae)
Rivulus spec. (Fam. Fundulidae)
Cichlasoma bimaculatum LINNÉ (Fam. Cichlidae)
Acaronia nassa HECKEL (Fam. Cichlidae)
Apistogramma spec. (Fam. Cichlidae)

This list must surely include only a small fraction of the species present, since the sampling method was not designed primarily with fishes in mind.

An indication of the amount of fishes which can accumulate under the floating vegetation under favorable oxygen conditions is presented below. GEISLER (1967, personal communication) collected the following species and numbers under an island in the Amazon near Ilha do Careiro (fig. 24, p. 68) composed of *Paspalum repens* and about 25 m^2 in area:

650 *Abramites microcephalus* NORMAN (Fam. Anostomidae)
40 *Leporinus spec.* (Fam. Anostomidae)
5 *Astronotus ocellatus* CUVIER (Fam. Cichlidae)
1 *Electrophorus electricus* (Fam. Electrophoridae) (length 1.2 m)
32 *Farlowella spec.* (Fam. Loricariidae)

Besides these, there were another 400 individuals in the family Characidae. The actual numbers present were doubtless much greater, for the mesh size of the net was too large for the catch to be considered quantitative.

In comparison, Amphibia were rarely taken. Only a few frogs and tadpoles were found.

Other animal taxa:

Specimens of Cnidaria, Turbellaria, Rotatoria, Nematoda and Hirudinea occurred in all biotopes, but were so rare as to be negligible. Bryozoa were more common, but they could not be sampled quantitatively due to their firm attachment to the substratum. Oligochaeta were represented at all stations by Naididae and Tubificidae; however, no large concentrations of the latter group, which are actually members of the benthos, were observed, Hydracarina were both very abundant and very diverse. In spite of the fact that this group is relatively well sampled (SIOLI, SATTLER, FITTKAU etc.) and many species have been described (VIETS 1954, BESCH 1964) the species lists are far from complete for them, too.

The species which represented most faunal groups were relatively small with the exception of the genus *Ampullarius*, there were no particularly large forms in any of the various families. On the other hand, the balance of this report will show that numbers of individuals were sometimes extremely high.

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[1] Identified by C. Meier-Brook, Univ. Tübingen

[2] Identified by H.A. Knoeppel, Würzburg

III. Quantitative investigations of the aquatic fauna

a) Methods

One or more samples were taken, usually at monthly intervals, from the floating vegetation at each station. A net designed especially for this purpose was used (fig. 1, photo 1). It consists of a collapsible, 2-m-long handle and a net on a frame 50 cm on each side. The netting has a mesh width of 223 microns. Finer meshes could not be used, because the frequently large amounts of organic detritus clogged the mesh openings.

To protect the fine netting, a shallower, removable bag was fitted into the mouth of the net. The sides of the inserted bag were of thick linen, and the bottom was wire screen with a mesh width of 8 mm. Coarser detritus and small aquatic plants were retained in the shorter bag.

Sampling was accomplished from a boat with the aid of an assistant. The net was shoved beneath the floating vegetation and lifted upwards out of the water with the long handle (photo 1).

Photo 1 : Sample drawing

The tangled mass of plants extending above the top of the net was chopped off with a bush-knife, then trimmed close to the rim of the net with a smaller knife. The remaining mat of roots and rhizomes was rinsed into the net and transferred to plastic bags for return to the I.N.P.A.[1] laboratory in Manaus, where it was treated further. All materials retained in the fine net were preserved in 70 % alcohol. The roots were washed again in the laboratory; depletion of oxygen in the bags during transport killed many sessile forms (especially Chironomidae), so that they could be rinsed more thoroughly from the roots. Direct examination of the root mass showed, however, that even this procedure did not remove all the animals. Nevertheless, the number of animals which was still in the roots was so low that the resulting error was negligible with respect to total abundance. Fractions which could not be washed out were 1 % for Copepoda, Cladocera, Conchostraca and Mollusca, and 2 - 5% for the rest. Materials which rinsed out into the net in the laboratory were preserved in alcohol and combined with the corresponding fraction obtained at the field station. Rhizomes were measured and the numbers of branchings, nodes and vegetative shoots were noted. The plants were dried to constant weight at 70°C.

To obtain samples in the inner portions of the floating mats of vegetation, a hole was carefully cut with a knife in the interwoven thatch of plants. A section was added to the lower end of the handle (fig. 1), for the stands were thicker in the central areas than on the periphery. Submerged bushes tore the net bag in such places, so an additional bag of stout linen was bound around the outside of the netting to protect it.

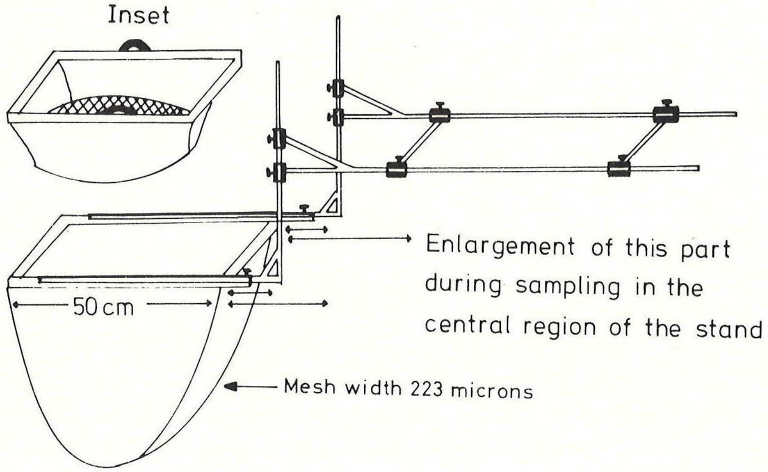
Inset
Enlargement of this part during sampling in the central region of the stand
50 cm
Mesh width 223 microns

Fig.1: Net construction

The sampling procedure was completely unsuccessful in very thick accumulations of several years' vegetation. Since only a few samples required the special procedure necessary to collect in these instances, the method will be described when the results of these samples are presented.

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[1] Instituto Nacional de Pesquizas da Amazônia.

The fauna was broken down for rough characterization into major groups, some of which included several systematic units. The only monospecific group was the Conchostraca: *(Cyclestheria hislopi* BAIRD*)*. That species will be given special emphasis because of its value as an indicator of certain ecologically important factors.

No attempt was made to count every animal in the samples, because of the large numbers of individuals and the frequently large amounts of detritus which had to be scrutinized in order to find them. Total abundaces were calculated from subsamples, assuming that the counts were normally distributed. The subsampling procedure consisted of pouring the well-stirred sample evenly over the bottom of a basin of known area. Best results were obtained when the water in the basin barely covered the detritus. Larger animals and pieces of detritus were removed from the samples before they were subsampled. Five subsamples were removed with a cylinder of known cross-sectional area, and these were counted and multiplied by an appropriate conversion factor to estimate total numbers. The standard error was on the order of +2 % [1].

The 95 % confidence limitis for larger groups were 10 %, and for the smaller, 15 % of the mean. Groups represented by only one specimen in the subsamples were recorded simply as ' + ', because of the statistical uncertainty of such low subsample counts. Similarly, absence of a group from the five subsamples does not allow for the conclusion that the group was not represented at the sampling station, since rare individuals could have been missed. On the other hand, groups not abundant enough to appear in the subsamples may be considered unimportant for purposes of the present investigation. The Conchostraca are again the exception; whenever there was any question about their absence, a more thorough examination was conducted. This was done because of their significance as an indicator organism in the study.

Numbers of animals in the samples were converted to abundance per m^2 to conform with standard practice.

Inability to separate all the animals from the detritus also prevented direct determination of the faunal biomass. A general estimate of biomass for comparative purposes was derived from the average weights of 500 individuals from each faunal group. Care was exercised in selecting animals to be weighed from the samples to utilize a representative cross-section of the species and sizes of individuals in the natural populations. These animals were dried to constant weight at 105°C to determine average dry weights. The results, expressed in terms of dry weight of 1000 individuals in each group, are as follows[2] :

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[1] Statistical analysis were undertaken by Dr. H. J. Krambeck, MPI Plön.

[2] The specimens had been preserved in 70 % alcohol for 1 - 2 years prior to weight. No correction for the influence of the preservative was attempted.

Copepoda	5.7 mg	Ephemeroptera	50.0 mg
Ostracoda	20.0 mg	Trichoptera	40.0 mg
Cladocera	3.5 mg	Diptera	25.0 mg
Conchostraca	38.0 mg	Hydracarina	15.0 mg
Hemiptera	50.0 mg	Mollusca	350.0 mg
Odonata	160.0 mg	Oligochaeta	13.0 mg
Coleoptera	120.0 mg		

These averages were used to calculate biomasses from counts of individuals.

As mentioned in the description of the subsampling procedure, all larger specimens of Hemiptera, Odonata, Coleoptera, Ephemeroptera, Diptera, Mollusca and all Decapoda were removed before subsampling in order to achieve as uniform a medium as possible and counted separately.

Since their numbers in the samples were small but their weights relatively large, substantial differences between sample biomasses occurred. Values were not representative of average biomass over an entire zone of vegetation, because aggregations or larger animals could have great influence on the estimates. Such aggregations were observed for *Macrobrachium amazonicum* and *Macrobrachium jelskii*, among others. To obtain total biomass, it therefore seemed more reasonable to us to calculate averages over many individual samples. Heavier animals, such as *Ampullarius spec., Macrobrachium spec.*etc. had longer life spans and thus were less affected by brief alternations in biotopic factors than populations of shorter-lived forms such as Diptera, Cladocera or Conchostraca.

These averages were calculated in the following manner. In the course of the investigations, it became apparent that 'floating meadows' could be divided into three fundamental types, based on their animal communities[1]. The numbers of individuals in samples from each of these types were determined. Subsequently, the average weight of a representative cross-section from each faunal group was calculated and converted to unit area of 1 m^2 (Table 1). This average weight was added in for each of the samples, and is given separately in the results for each station. In this manner, the singly occurring, large and heavy individuals were included without introducing a large error into the estimates of biomass.

Since many authors give biomasses in terms of fresh, or wet weight, an approximation of this value will also be given here. Simple conversion of dry to wet weights is subject to large errors due to differences in the average water content of various faunal groups. HARNISCH (1954) reports that chironomid larvae from Germany have proportions of 11 - 17 % dry weight per unit weight. Mr. POLTZ (unpublished data) has determined that the dry weight of zooplankton in Holstein lakes amounts to 10 - 12 % of the fresh weight. In order to obtain at least a crude estimate of wet-weight biomass, we have decided that conversion factors of 7 and 6, depending on the proportion of dry weight due to Crustacea or Insecta respectively, provide credible estimates of these data. The proportions of dry in wet weight to which these factors correspond are 14.3 and 16.7 %. They are not valid for the Mollusca, however, since the proportion of dry weight is greatly increased by their shells. Cursory weighings indicated that dry weights of mollusks are about one-third of the wet weights (alcohol-preserved material). Dry-weight biomasses of mollusks were appropriately multiplied by 3 in the calculations of wet-weight biomasses.

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[1] A summary of the logic behind the erection of these types is given on p. 86 ff.

Biotope 1 (Whitewater Type)[1)]
Paraná do Xiborena, Costa do Baixio lotic region,
lotic region of the Amazon.

Biotope 2 (Lago Type A)[1)]
Lago Calado, Lago Manacapurú, Lago do Xiborena, Lago dos Passarinhos peripheral region[2)], Lago Parú , Lago Castanho, Costa do Baixio shore region.

Biotope 3 (Lago Type B)[1)]
Lago dos Passarinhos central region, Lago Parú, Lago Castanho.

Table 1 : Average weights of the larger individuals, which were picked from the samples before subsampling, in each biotope.

Animal Group	Average Weight (g/individual)	Total Number in Biotope 1	Total Weight in Biotope 1 (g)	Total Number in Biotope 2	Total Weig in Biotope 2(
Decapoda	0.031	12	0.372	548	16.988
Hemiptera	0.082	4	0.328	53	4.346
Odonata	0.016	21	0.336	394	6.304
Coleoptera	0.013	–	–	23	0.299
Ephemeroptera	0.004	–	–	43	0.172
Diptera	0.028	–	–	13	0.364
Mollusca	0.174	6	1.044	194	33.756
		Sum	2.080		62.229

There were no larger specimens in Biotope 3.
Number of samples (= 1/4 m^2): Biotope 1 : 40
Biotope 2 : 112

Average biomasses of pre-sorted individuals per m^2:

Biotope 1: 0.208 g dry weight (= about 1 g wet weight)
Biotope 2: 2.222 g dry weight (= about 10 g wet weight).

[1)] A summary of the logic behind the erection of these types is given on p. 88 ff.

In the vegetation, a marginal region and a central region were distinguished. The marginal region was that part of the stand which bordered the open water surface. It was characterized by lower densities of plants, penetration of solar radiation between the roots, colonization of the roots by sessile algae and good exchange of water with the surrounding medium. The central region was that in which the plants formed an uninterrupted cover over the water and the stand approached its ultimate natural thickness. Depending on the growth form of the vegetation, the peripheral zone ranged from a few centimeters (dense floating islands) to several meters in width. In Lago Calado, in 1968 for example, the distinction between peripheral and central zones was not apparent until July, for the development of the vegetation did not reach a characteristic condition before that month.

The investigations were mainly concentrated in *Paspalum repens* in order to minimize substratal variation. This plant was also well suited to the sampling method, in that the stands did not usually reach to the bottom, and its stands were the most widely distributed of the grasses in the 'floating meadows'.
Stands of *Echinochloa polystachya* were normally rooted to the floor of the supporting body of water, were generally too sparse for the size of net which was used, and were difficult to handle because of the thick, hard rhizomes. A few exploratory samples indicated that stands of this grass offered no significant additional insight with regard to present goals.

Transparency was estimated with a Secchi disc, and current speed was determined by timing floating objects with a stopwatch.
Oxygen concentration was determined by the Winkler method. In order to avoid disturbing vertical stratification of the water in the stands, samples for this purpose were taken with a tube 3 mm in diameter which was pushed down to the desired depth (a modification of the method given by MILBURN & BEADLE 1960).

Characterization of each of the biotopes, as well as discussion of the environmental factors which are important to the faunal communities will be based on Copepoda, Cladocera, Conchostraca, Ephemeroptera, Trichoptera and Diptera, since these groups showed the clearest relationships. Other groups (Decapoda, Hemiptera, Odonata, Coleoptera, Hydracarina, Mollusca, Oligochaeta, Hirudinea) are included in the treatments of total abundance and total biomass.

b) Sampling stations

1. Paraná do Xiborena

Description of the biotope:

The Paraná do Xiborena is a winding canal about 50 m wide which connects the Rio Negro to the Rio Solimões below Manaus (fig. 2). It dries up during the period of low water in October and November. As water levels rise, whitewater flows in from the Solimões and blackwater from the Rio Negro, so that the water is practically motionless in the middle parts of the canal in December and January. At that time, the water has a loamy, yellowish color with a faint greenish tint and a strongly developed pleuston.

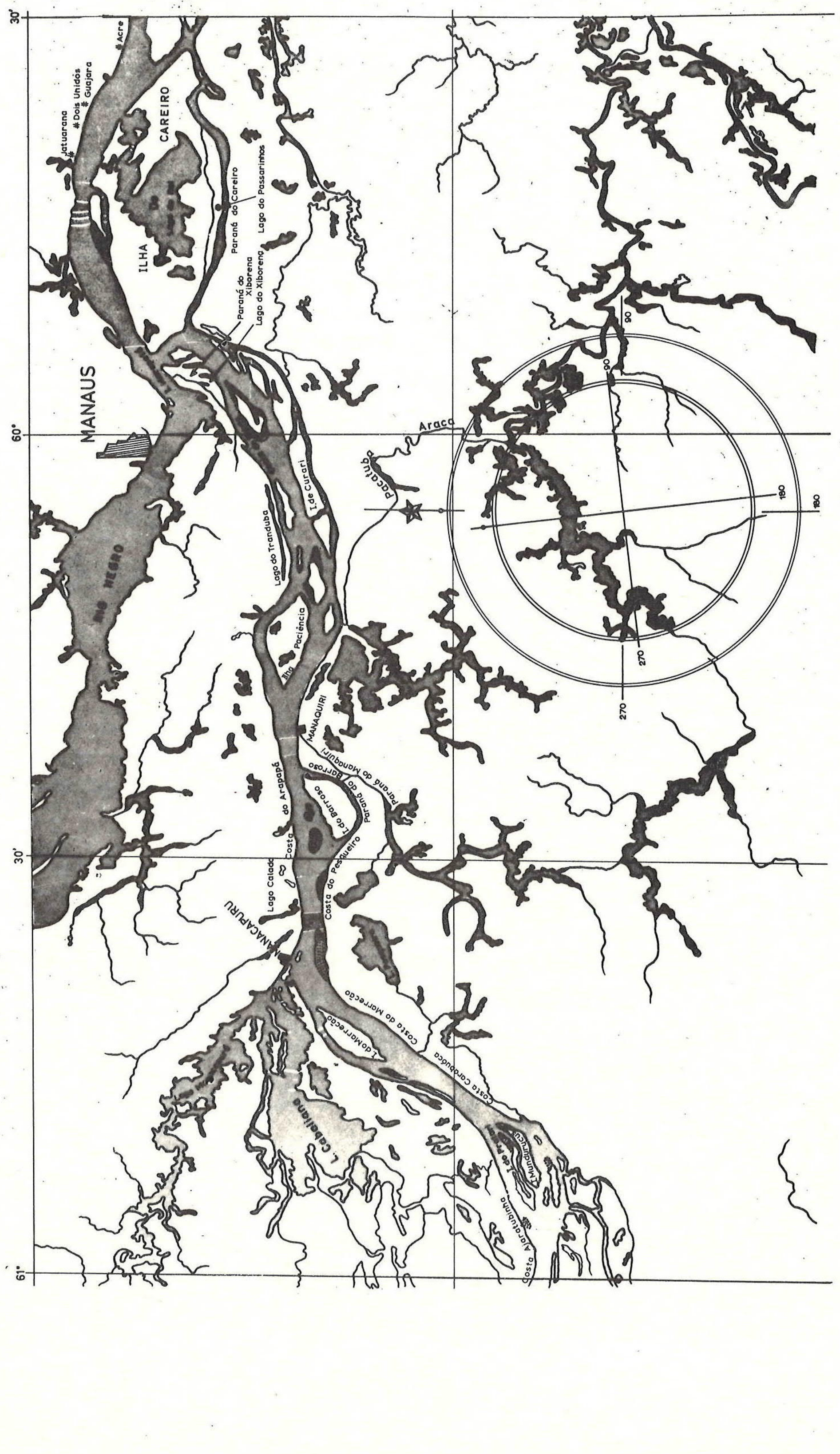

Fig.2: Map of the investigated area (copy from I.N.P.A.)

During this period, rapid growth of *Paspalum repens, Pistia stratiotes, Salvinia auriculata* and *Azolla spec.* occurred over the entire water surface. By March, the water had risen high enough so that a distinct current toward the Rio Negro was in evidence, even close to the banks. The current had carried away most of the floating vegetation. There was only a narrow strip of *Paspalum repens* and *Echinochloa polystachya* about 1 - 5 m in breadth near the banks (photo 2). From that month on, therefore, this station represented the sort of biotope which was described in Part I for the sedimentation and shore zones of the Solimões-Amazon. The plants grew intensively throughout the year and were always in the young stages with vesicular leaf-discs.

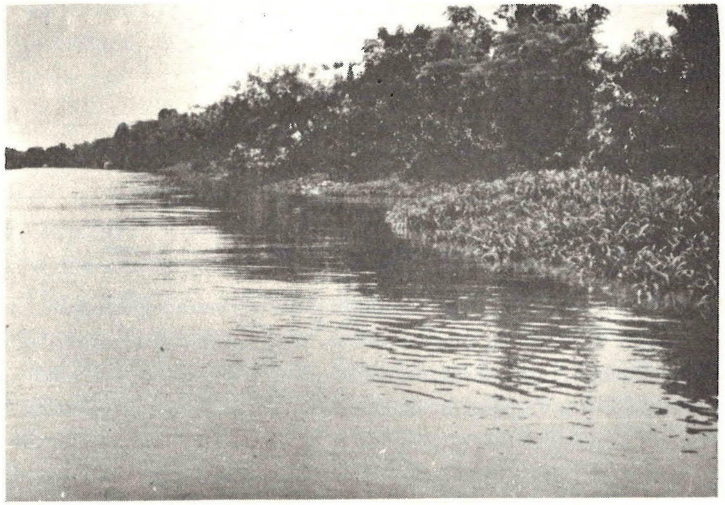

Photo 2: Small *Paspalum repens* population (Paraná do Xiborena).

Because of the current and constantly changing water levels, parts of the stand were often washed away. Samples could therefore be taken repeatedly along the same part of the shore without being from the same portion of the stand. The central, or internal parts of the stand were not sampled because the strip of plants was too narrow and was anchored in submerged shrubs along the banks.

Physical-chemical-investigations:

The surface temperature of the water near the plants varied between about 29°C and 34°C depending on the time of day and weather during the stagnation period in December and January. From February to the end of the investigations, it varied between 27°C and 29°C as a result of water movement. Conductivity and pH measurements show that the Paraná do Xiborena was continually under the influence of whitewater (fig. 3). The pH values

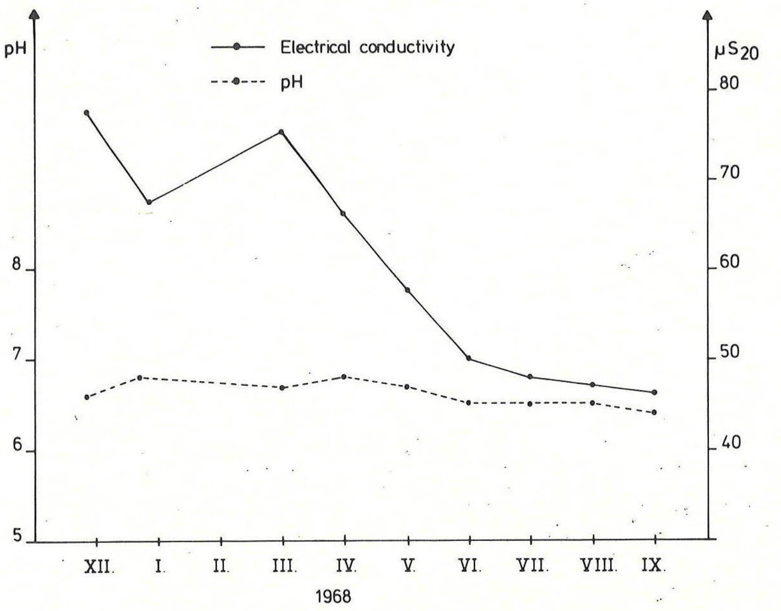

Fig.3: Paraná do Xiborena: pH-value and electrical conductivity in the course of the year

were virtually constant. In contrast, electrical conductivity values were highest from December, when measurements were begun, through March, then showed a clear decline. BRAUN (1952) recorded similar events in his investigations of the chemistry of lakes along the lower reaches of the Rio Tapajós. He attributed the changes to the effect of decomposing plants which were killed when rising water levels flooded them. Also, the areas of the lakes increase considerably, and salts which are dissolved from the flooded soil could contribute to the increases in conductivities. In lakes with affluents, this process of salt enrichment can be more strongly expressed if the inflowing streams have previously flooded over extensive land areas. This complex process, which BRAUN designates by the conceptual term 'shore factor' (Uferfaktor), acts in opposition to the diluting effects of increasing water volume, or 'dilution factor' (Verdünnungsfaktor). The 'shore factor' must surely be even more significant in the enrichment of várzea lakes by electrolytes, because of the way in which sinking water levels leave large quantities of floating vegetation stranded on dry ground. During the dry season, this material is extensively remineralized and the resulting soluble ions can then have a strong influence on the chemistry of the water when the dry areas are flooded again (McLACHLAN 1971). In our opinion, still another process besides this leaching of shore areas adds to the sources of electrolytes-regeneration from lake-bottom muds. Such regeneration is independent of the course of rising water levels, and is most effective when the total volume of a body of water is relatively small.

A particularly good example of this process exists in the Lago do Xiborena, whose water had a conductivity of more than 300 μS_{20} in the period of low water levels. The significance of the mud for the chemistry of the water will be taken up in more detail in the discussion on that lake (p. 68 ff.).

The relatively high electrolyte concentrations in the Paraná do Xiborena during low water levels must have been due mostly to the 'shore factor', however. This is because the canal contained rapid currents over 8 - 10 months of the year which prevented the deposition of significant quantities of organic muds. Shore leaching was mainly accomplished by rainfall. In addition, a confluence with the Lago do Xiborena was re-established in December. Conductivities in this backwater, as mentioned above, had risen above 300 μS_{20}. Changing water levels in the following months effected a slow exchange of water with the canal. In this case, still another source of electrolyte enrichment cannot be totally disregarded: grazing cattle belonging to people living along the banks of the várzea.

Transparency was very low during the entire period, but as a result of fundamentally different factors (Table 2). The particularly high turbidity observed during the first months could not be accounted for to any great extent by the continuing addition of suspended inorganic matter by the whitewater inflow, because the current was too slow. Rather, the shallowness of the water (about 1 m) allowed slight wind action, the activities of large fishes, etc. to stir up the bottom and maintain fine detritus and inorganic material in suspension. This phenomenon was observed in all lakes in which the water level sank low enough (Lago Calado, Lago do Xiborena etc.). The transparency could decrease to less than 10 cm under certain wind conditions. Beginning in March the cause of the turbidity became the suspended inorganic load of the whitewater inflow, which was kept in suspension in the canal by the currents. As a result, distinct changes in the environmental factors took place in the Paraná do Xiborena, in spite of continuing high turbidity.

Table 2 : Transparency and current speeds at the station in the Paraná do Xiborena

	1967			1968								
month	VIII.	IX.	XII.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.
transparency (in cm)	40	45	30	30	–	20	30	40	40	50	40	30
current speed (in cm/sec.)	25	25	+	+	–	10	15	+	5	15	15	20

The faunal community:

The difference between the effects of stagnant, turbid water and flowing, turbid water was clearly evident in the aquatic biota. Although flowing whitewater with a transparency from about 30 to 40 cm supports little if any autochthonous phytoplankton (GESSNER 1959), these organisms could be quite abundant during December and January in essentially stagnant bodies of water with similarly low transparencies. This was shown with membrane-filter preparations by SCHMIDT (1971). The effect on the fauna was also clearly marked.

The maximum absolute density of individuals occurred in December. As the influence of pure whitewater increased, phytoplankton decreased and the density of animals declined (fig. 4 a). In the data for the separate faunal groups, it can be seen that the filter-feeding Cladocera decreased sharply (fig. 4 e). A critical change in the ratio of usable to indigestible suspended matter occurred as fresh whitewater flowed in. The rare Conchostraca were present only in December, when the Cladocera were going through their maximum. Another unfavorable factor was the current itself, which carried away the unattached animals. All other groups but the Copepoda and Ostracoda, which also had maximum densities in the early stages of community development, were rare (fig. 4 c, d).

Sessile forms, such as Diptera and Trichoptera, and the Ephemeroptera, which are strong swimmers, showed no adverse reactions to the current, and were able to continue toward later maxima (fig. 4f, g, h). In addition, these groups could make better use of the "Aufwuchs" on floating vegetation and detritus trapped in it as food sources. It appears, and this is supported by other investigations, that the community as a whole in lotic situations responds less to the large-scale rhythms such as high and low water periods, than to local current conditions. Since environmental conditions in the Paraná do Xiborena were dominated by the effects of flowing whitewater in all months but December and January, it seemed justified to ignore the chronological differences among these samples and determine the mean total abundance for the community as a measure of the average faunal density in this biotope. This quantity was 15300 individuals per m^2 in the marginal region.

The above findings suggest that higher abundances could be expected in the parts of the stands which were more protected from the current, nearer the banks. Samples which would have substantiated this could not be taken because of the submerged shrubs in those parts. Biotopes discussed later, in which such samples were taken, did support this assumption.

Generally, the density of animals in this community remained low in comparison to the other biotopes.

Figures for total biomass give a somewhat different impression (fig. 4 b). The maximum biomass was not contemporenous with maximum abundance, because the peak biomass was due to heavier, rarer forms, especially Mollusca. In other words, the biomass was

Fig. 4 a - h: **The aquatic fauna in the floating vegetation of Paraná do Xiborena in the course of the year.**

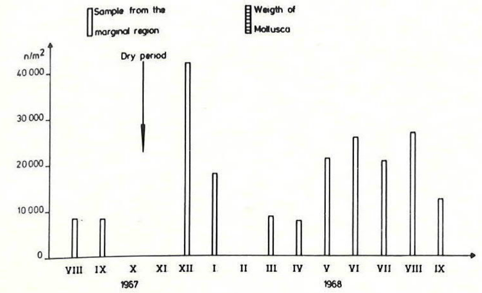

Fig.4a: Total number of individuals

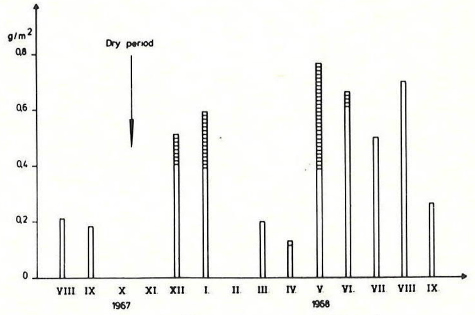

Fig.4b: Total dry weight (without large individuals)

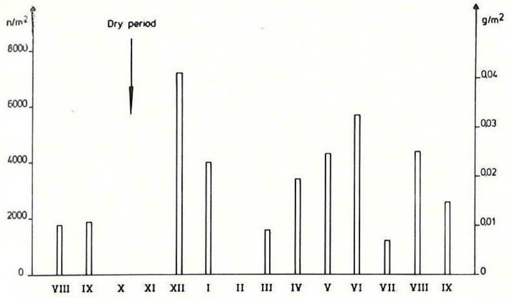

Fig.4c: Copepoda

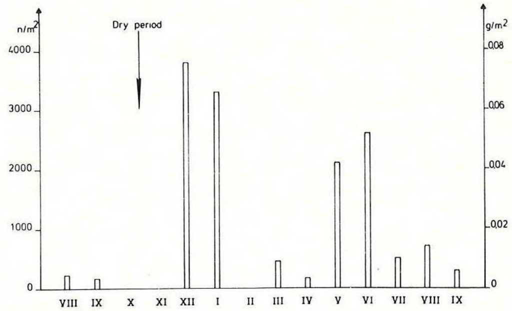

Fig.4d: Ostracoda

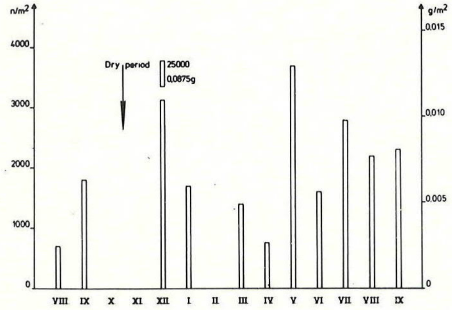

Fig.4e: Cladocera

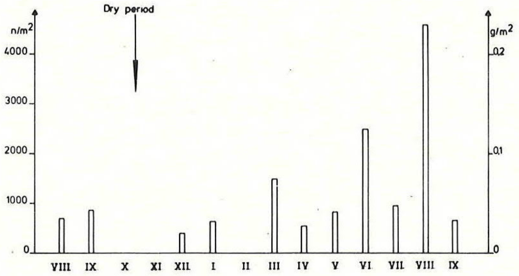

Fig.4f: Ephemeroptera

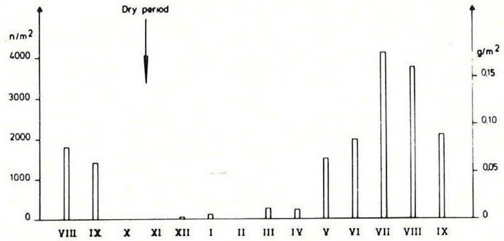

Fig. 4g: Trichoptera

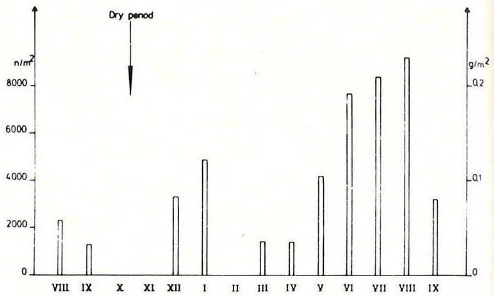

Fig. 4h: Diptera

strongly influenced by an animal group which occurred in relatively small numbers, irregularly distributed, and whose abundance within the bounds of the present investigations was of no value for indicating changes in biotopic conditions. In contrast, such changes had very marked effects on abundances of the more numerous, shorter-lived animals which contributed little to total biomass. Therefore, abundance will be given more weight than biomass in discussing our results. Also, the proportion of total biomass due to Mollusca is illustrated by cross-hatching on the biomass curve in figure 4 b.

Samples from December and May may be compared for an illustration of this discrepancy. Analysis of total abundances indicates a fundamental difference between the biotopic conditions in these two months, and this was clearly apparent in the field. In December, the dominant conditions were those of a very shallow lake, while in May, flowing whitewater was the primary factor. As will be shown below (see p. 88) abundances and, normally, biomasses per m^2 were significantly higher under the conditions which were dominant in December than in flowing whitewater.

The biocenosis corresponding to the former condition could not develop fully because the biotic conditions were of too short duration. For example, the Conchostraca, which occurred in all standing waters and usually in great abundance[1], were rare at first. Only Cladocera and other short-lived, smaller forms were able to increase in number and to so reflect the biotopic conditions precisely; even so, it is probable that these groups did not reach the maximum abundance possible under those conditions. Cladocera responded rapidly to the establishment of whitewater flow in May: their numbers declined sharply (Table 3).

Although the numerical decline in this group was clearly evident, the decrease in their biomass relative to that of the entire fauna was far less striking. The changes in Mollusca were just the reverse - their numbers rose relatively little, but their biomass increased considerably. As a result, total biomass increased as total abundance was decreasing! As has already been mentioned, the abundance of Mollusca in these investigations was not useful as an indicator of biotopic conditions, and their occurrence was highly irregular. Therefore, conclusions about the relationship between biomass and biotope can be misleading. Rather, clues to biotopic events are better found in data on abundance.

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[1] See p. 88 ff.

Table 3: Proportions due to Cladocera and Mollusca in the total abundance and total biomass exclusive of larger individuals removed before subsampling.

Month	Total Abundance (no./m^2)	Abundance of Cladocera or Mollusca (no./m^2)	% of Total Abundance	Total Biomass (g/m^2)	Biomass of Cladocera or Mollusca (g/m^2)	% of Total Biomass
			Cladocera			
December	41 520	25 000	60.2	0.515	0.088	17.1
May	21 060	3 700	17.6	0.776	0.013	1.7
Difference	20 460	21 300	42.6	0.261	0.075	15.4
			Mollusca			
December	41 520	330	0.8	0.515	0.116	22.5
May	21 060	1 100	5.2	0.776	0.385	49.6
Difference	20 460	770	4.4	0.261	0.269	27.1

In order to obtain the total biomasses for the samples, it is necessary to add the mean dry weight due to larger specimens which were removed before subsampling to the amounts in Table 3. This value is 0.208 g[1]. Total biomass in this biotope therefore fluctuated between 0.3 and 1.0 g dry weight per m^2. This is equivalent to a wet, or fresh weight of 2.0 - 6.0 g/m^2, when the part of the dry weight due to Mollusca is calculated specially [2].

As was brought out in the discussion of abundances, the mean of all samples taken during the time of a dominating whitewater influence (i.e., excepting those in December and January) best represents the average faunal density in the marginal region of the stand. Including the larger, pre-sorted animals, the corresponding estimate of mean biomass is 0.61 g dry weight per m^2. The equivalent wet weight would be about 3.5 g/m^2.

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[1] See p. 19 f. for the derivation of this quantity.

[2] See p. 19 f. for the procedure used to calculate wet weights from dry weights.

2. Costa do Baixio

Description of the biotope:

The Costa do Baixio is a sedimentation zone several hundred meters wide and several kilometers long on the left bank of the Rio Solimões about 20 km above the mouth of the Rio Negro (fig. 2). The area is dry land from December to January. The higher portions are covered mainly by *Echinochloa polystachya* and *Paspalum fasciculatum,* and the highest places are colonized by *Salix humboldtiana.* Scattered *Hymenachne amplexicaulis* and *Panicum chloroticum* also occur there. At the start of the dry season, *Paspalum repens* is still very evident, but it rapidly transforms entirely into the very dissimilar land form. Inhabitants of the region use this area for cultivating jute (*Corchurus capsularis*) and vegetables, in the course of which portions of the natural grass crops are cleared away.

In February 1967, a strong development of *Paspalum repens* began as the water rose. *Echinochloa polystachya* and *Hymenachne amplexicaulis* also grew rapidly. Within about 2 1/2 months the stand attained its largest areal extent, about 4 km^2. In May, increasingly large portions of the stands, especially those of *Paspalum repens,* were torn off the peripheral zone and carried away by higher water levels and increasing current speeds. Stormy weather augmented the process during this period, as exposed parts of the stands were broken off or severely damaged by wave action. From August on, only small patches of *Paspalum repens* remained along the banks. The rhizomes of *Echinochloa polystachya* jammed together so tightly as the water receded that it was no longer possible to take samples from the inner parts of the stands.

Station 1 (lotic region)

Station 1 lay unprotected from wind or current on the extreme outer margin of the stand (fig. 5). May samples had to be taken in a somewhat less exposed area because the storms had severely damaged the outermost *Paspalum repens* stands and disturbed their natural structure. As in the Paraná do Xiborena. the location of the station in this biotope was always the same, but the stand under investigation changes considerably from month to month.

Physical-chemical investigation:

The temperature of the water was between 27°C and 29°C all year. There was no diurnal stratification. Near the grass, the current was very slow. Often the turbulence was so great that no directional current could be measured with the method used. Higher values were observed only in August and September (Table 4).

Transparency was somewhat higher here than in midriver (Table 16).

Conductivities were markedly influenced by the "shore factor" as the water began to rise, because the gradual slope of the sedimentation zone resulted in the flooding of large areas with relatively minor increases in water level. In addition, large amounts of vegetation were decomposing, including jute, which had been submerged in shallow water to allow the fibers to loosen (maceration). As early as May, the "dilution factor" gained precedence:.

Table 4 : Transparency and current speed [1] on the Costa do Baixio (lotic region) and in the lotic zone of the Amazon.

Costa do Baixio

1968 Month	III.	IV.	V.	VI.	VII.	VIII.	IX.
Transparency (cm)	35	30	40	50	45	45	45
Current speed (cm/sec.)	+	+	+	+	+	10	20

Amazon (lotic zone)

	III.	IV.	V.	VI.	VII.	VIII.	IX.
Transparency (cm)	25	25	35	–	40	40	–

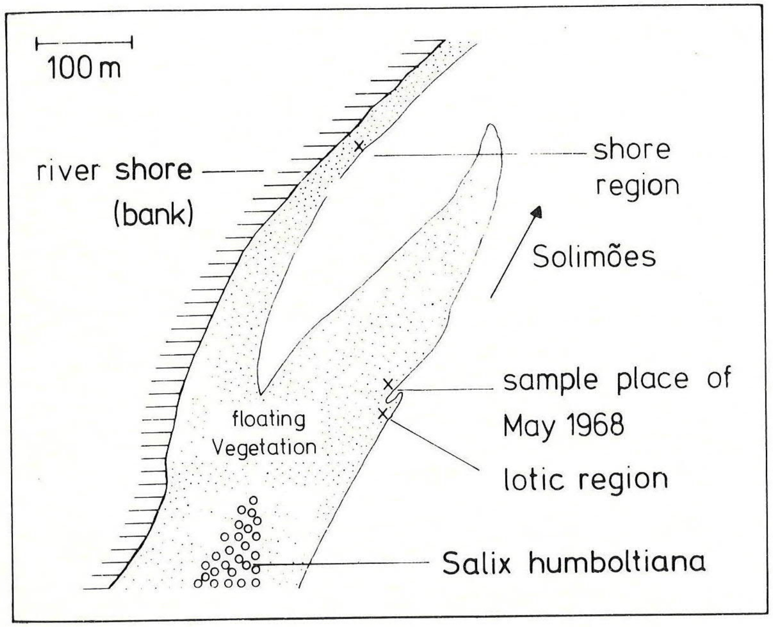

Fig. 5: Costa do Baixio (Schematic)

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[1] Since the vegetation was drifting, no current speeds could be given for the Amazon.

conductivities fell. Beginning in June, the effects of the "shore factor" were no longer evident (fig. 6). Values of pH increased until May, from 5.9 to 6.8, then fell to 6.5 in June and varied between 6.4 and 6.6 thereafter (fig. 6). Even here, the "shore factor" was effective until May.

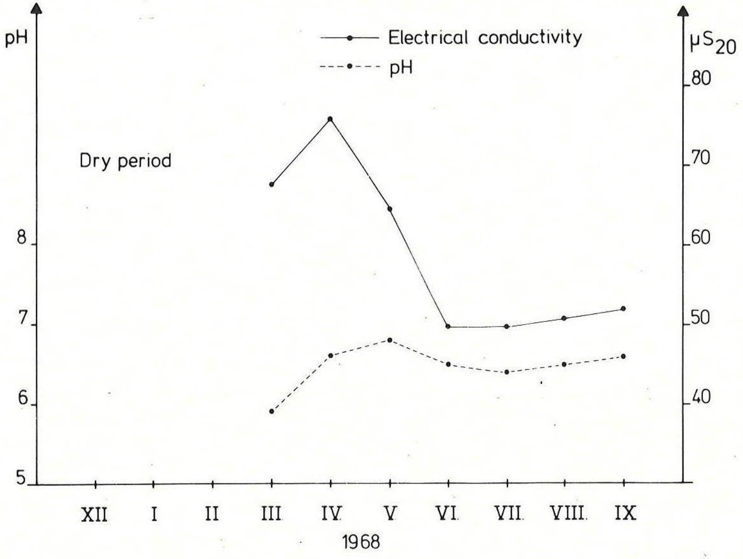

Fig.6: Costa do Baixio: pH-value and electrical conductivity in the course of the year

The continual, if slight exchange of water through the inner parts of the stands was sufficient to prevent oxygen depletion, so there was plenty of available oxygen there (Table 5).

Table 5 : Oxygen concentrations in the *Paspalum repens* stand of the Costa do Baixio (lotic region).

	Oxygen Concentration (mg/l)			
Depth (cm)	Open Water	Periphery of the Stand	5m Inward	15m Inward
0	4.53	4.30	4.43	4.57
		4.48		4.56
40	--	4.19	4.15	4.26
		4.32	4.17	4.06

The faunal community:

Here, too, a distinct dependency of total abundance on current speeds is evident when the two sets of data are compared (fig. 7a). In August and September, abundance was least as the highest current speeds were measured. (Table 4).

The strikingly high total abundances in May were at least partly due to the sheltered locations within the stand from which the samples were taken. The outer, more exposed vegetation had been damaged by strong currents and the natural biotopic structure had been extensively disturbed (fig. 5). Of the separate faunal groups, the Crustacea showed the most definite responses to changes in current conditions in terms of relative abundance, just as in the Paraná do Xiborena. Such numerical responses were weaker or non-existent for Ephemeroptera, Trichoptera and Hemiptera (fig. 7).

Fig. 7a - h: The aquatic fauna in the floating vegetation of Costa do Baixio (lotic region) in the course of the year.

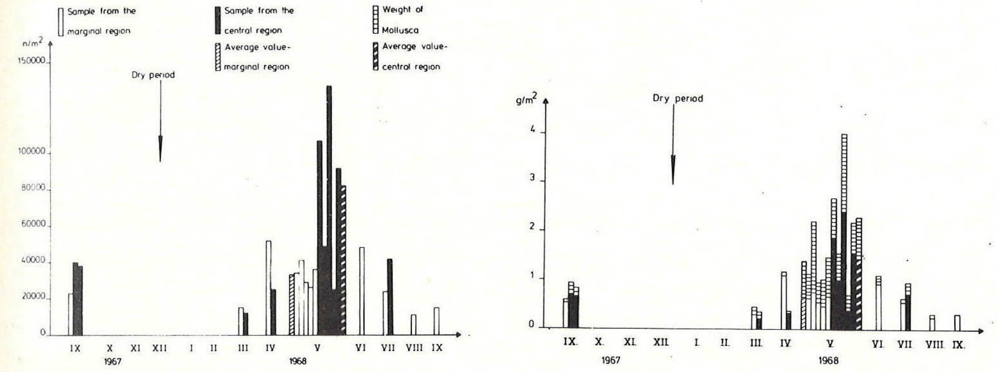

Fig.7a: Total number of individuals

Fig.7b: Total dry weight (without large individuals)

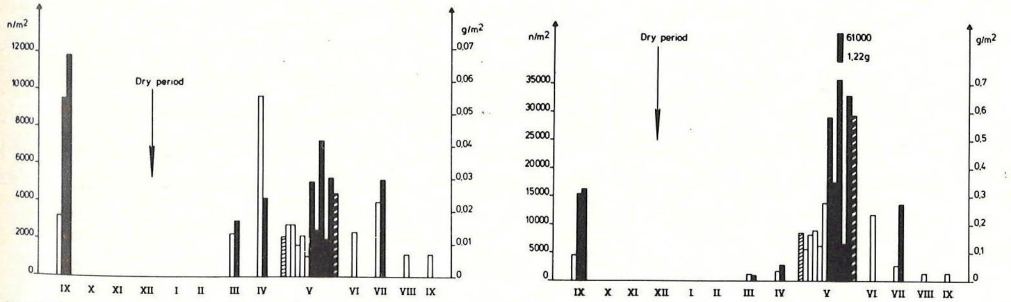

Fig.7c: Copepoda

Fig.7d: Ostracoda

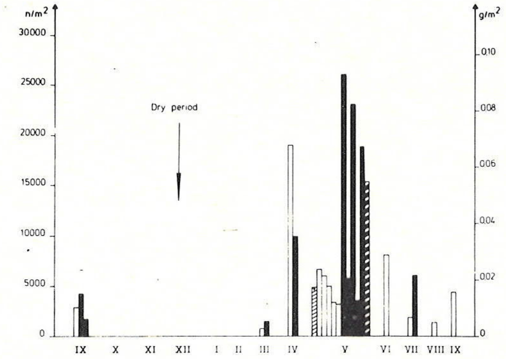

Fig. 7e: Cladocera

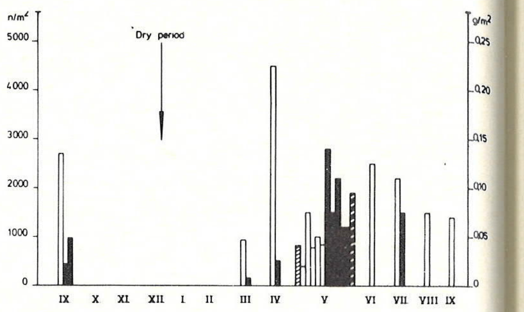

Fig. 7f: Ephemeroptera

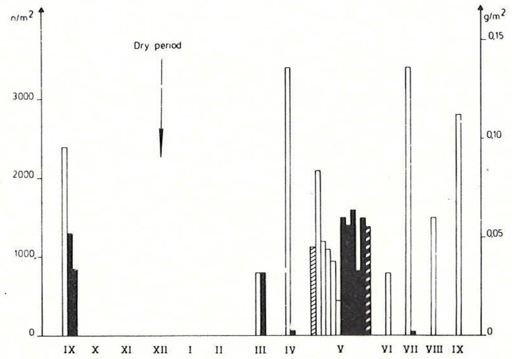

Fig. 7g: Trichoptera

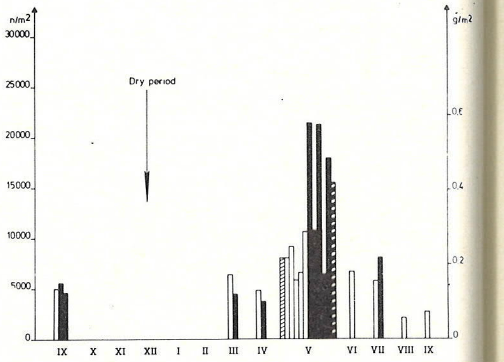

Fig. 7h: Diptera

Comparison of several parallel samples revealed, however, that rather large differences in relative abundance existed at adjacent sites. In May, 1968 five samples were taken on the periphery and five more about 10 m away in the inner part of the stand. Samples in each set were 10 - 20 m apart. Those from the inner part of the stand exhibited especially great differences. In order to quantify the amount of biotope in each sample more precisely, rhizome lengths were measured, root-knots were counted and the dry weight of the roots was determined (fig. 8). There was no marked correlation between these attributes of the root mass and abundances of animals. Lower abundances sometimes coincided with a lesser amount of roots, but any clear relationship was obliterated by local aggregations of one species or another. It must be conceded that the methods we employed were not precise enough to detect possibly significant local differences, for example, in the amount of turbulence, spatial distribution of the roots, structure of the surrounding area, light conditions etc. which could affect the fauna. Only in extreme cases was the amount of roots clearly limiting to the community.

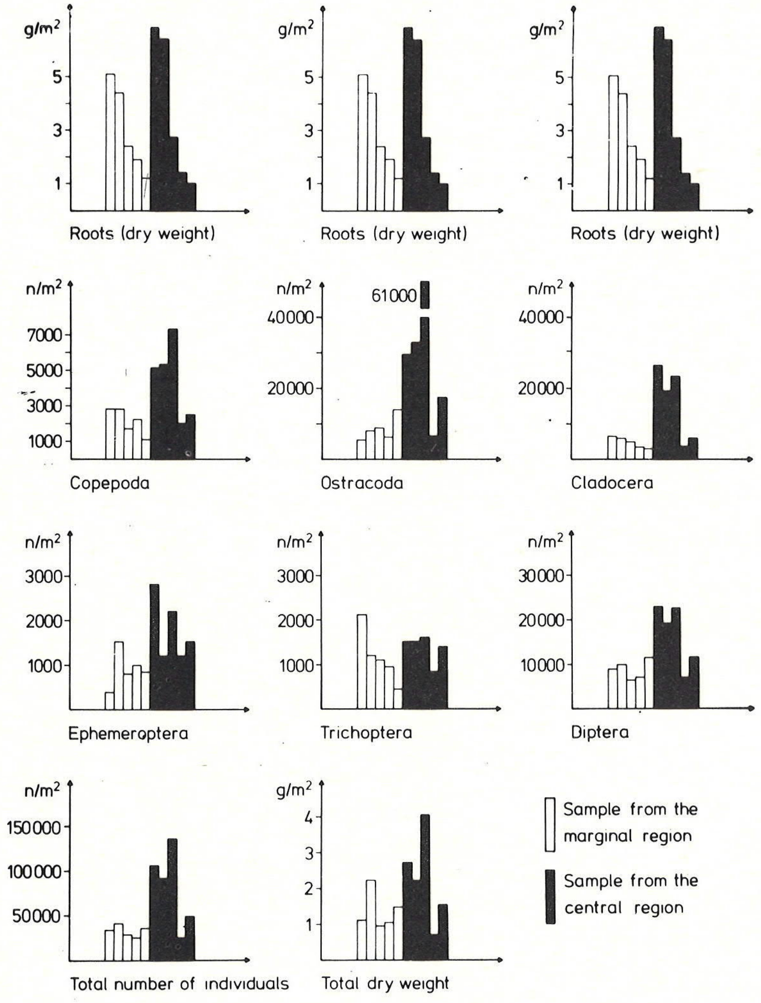

Fig 8: Roots (dry weight) and total number of individuals (3.5.68 Costa do Baixio)

Mean total abundance in the five marginal samples was about half the mean total for the five from the central zone. In order to establish that a significant faunal increase toward the center existed, however, a larger number of samples would be required because of the variability of abundances among them.

The separate faunal groups showed the following tendencies: abundances of Copepoda, Ostracoda, Cladocera and Diptera were generally higher in the central zone than on the periphery. No definite preference for either periphery or center was evident for Trichoptera or Ephemeroptera. Hemiptera usually decreased in abundance toward the center.

An explanation for this pattern, as has already been mentioned, may be found in the effects of the current. While the margins of the stands are fully exposed to whatever turbulence is present, the inner portions are protected by intervening roots and rhizomes, and the likelihood that the small Crustacea will be carried away by the current is reduced: their numbers increase. The same is possibly true for the Diptera. The abundances of Trichoptera, Ephemeroptera and Hemiptera are not particularly affected by the current, since they can either attach firmly to the roots or are strong swimmers.

The fauna is apparently under the dominating influence of local current differences in this biotope, as in the Paraná do Xiborena. It seemed justified, therefore, to again ignore the temporal differences among the samples and to derive a mean abundance from all samples in the peripheral zone for comparison with the mean of central zone samples and for the central zone, about 57 000 per m^2 (fig. 9). The graph of biomasses illustrates a pattern almost identical to that for abundances (fig. 7 b). The exceptions were two samples from the marginal region in May; the biomasses in these samples were much higher relative to abundance than for the other samples. The excess was due to Mollusca. Higher biomass values from the central zone of the stand had the same cause. The range of biomasses, like the range of abundances, was very large.

Total biomasses are calculated from dry weights given in the graphs by adding the average weight of larger animals from all samples – 0.208 g[1]. The biomasses in the lotic region of the Costa do Baixio varied from 0.5 to 2.4 g dry weight per m^2 on the periphery, and between 0.6 and 4.2 g per m^2 in the central zone. The equivalent wet weights[2] were about 3 – 14 g/m^2 on the periphery and 3 – 20 g/m^2 in the central zone.

As has already been intimated in the discussion of abundances, the condition of the fauna on the Costa do Baixio, too, depends primarily on local currents. The average for all samples will therefore give the most representative picture of faunal populations in the stand as a whole.

According to this, the following values are indicative of faunal biomass (including the larger specimens):
Mean dry weight in the marginal region: 1.15 g/m^2.
Mean dry weight in the central region: 1.66 g/m^2.
These values are equivalent to wet weights of about 6 and 8.5 g/m^2
(fig. 9).

[1] See p. 19 f. for the calculation procedure.

[2] See p. 19 f. for the procedure used in calculating wet weights from dry weights.

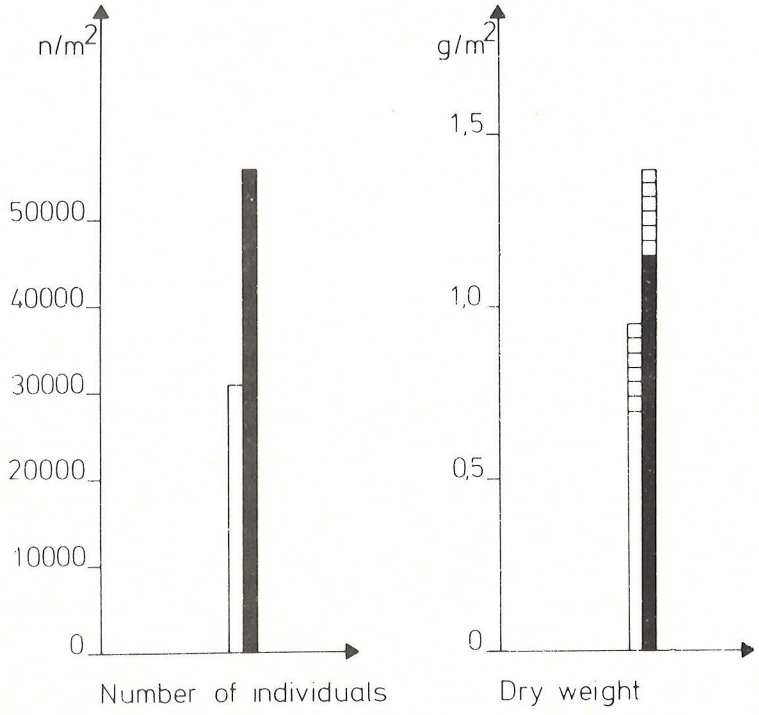

Fig 9 Costa do Baixio (lotic region)· mean values of all sample

Station 2 · shore region

Physical-chemical investigations:

Station 2 lay near the shore, protected by the masses of intervening plants (fig. 5). Current was very greatly reduced and transparency increased to 60 - 65 cm. On calm days, there was even a slight thermal stratification. On those occasions the temperature at the water surface was about 0.5^{0} higher than at a depth of 40 cm. Under these conditions, it is very possible that some autochthonous phytoplankton development occurred. The *Paspalum repens* stand at the station was present from May until the area dried up in September. It was rather dense and showed definite evidence of senescence at the end of that period (JUNK 1970).

The faunal community:

Total abundances were much higher at this station than at station 1 (fig. 10), possibly excepting the month of May. The May sample, however, was taken before environmental conditions had fully reached the levels of the following months: A slight current was present. Further evidence that the environment was still in a state of transition can be seen in the failure of Conchostraca to appear before June.

Fig. 10a - i: The aquatic fauna in the floating vegetation of Costa do Baixio (shore region).

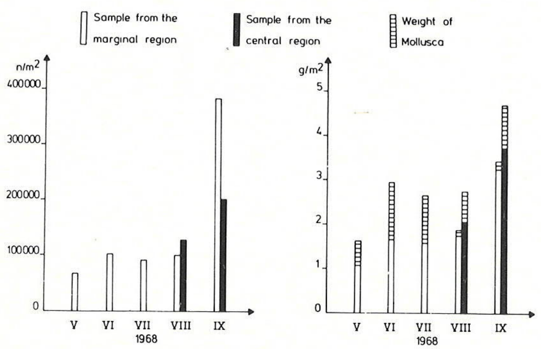

Fig.10a: Total number of individuals

Fig.10b: Total dry weight (without large individuals)

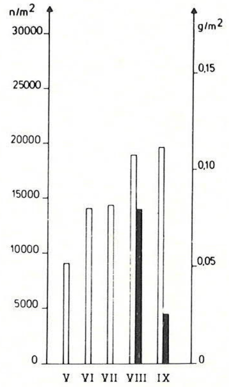

Fig.10c: Copepoda

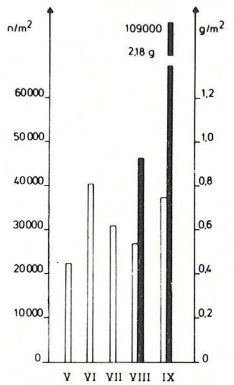

Fig.10d: Ostracoda

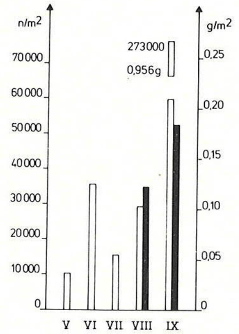

Fig.10e: Cladocera

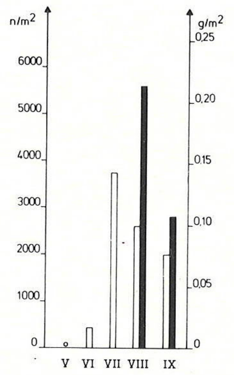

Fig.10f: Conchostraca

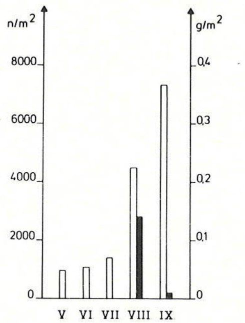

Fig.10g: Ephemeroptera

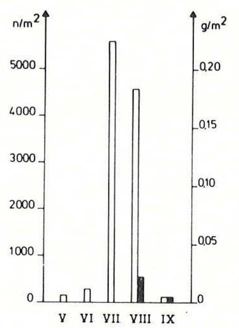

Fig.10h: Trichoptera

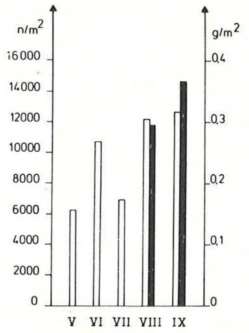

Fig.10i: Diptera

As previous investigations have shown, these filter-feeders are absent or very rare in flowing whitewater with full loads of sediments. Their regular occurrence in the shore region thus represents a new element in the faunal community. The maximum total abundance occurred shortly before the biotope dried up. At this time, the water was completely still. Filter-feeding Cladocera multiplied with amazing speed in September (fig. 10 e).

Since only two samples were taken from the center of the stand at this station, no conclusions can be drawn about differences in abundance between periphery and center. In those samples, Ostracoda and Conchostraca were more abundant in the central zone, while numbers of Ephemeroptera, Trichoptera and even Copepoda were much greater in the outer part (fig. 10, c - i).

Changes in biomass mirrored those in abundance. Only the September samples were very different (fig. 10 b). Abundance was greater in the outer parts of the stand, while biomass was greater toward the center. This was due mostly to Ostracoda, which were much more abundant in the central zone and are considerably heavier than Cladocera. The decline in total abundance, caused largely by a decrease in Cladocera, did not show up in the biomass.

The average weight of larger specimens, which must be added to the dry weights given in the figures to obtain total biomass, was 2.2 g/m^{2}at this site[1].

Biomass increased from 3.8 g/m^2 in May to 5.6 g/m^2 in September on the outer edges of the stand, and even higher - to 6.9 g dry weight per m^2 - in the central zone.

These values are equivalent, when calculation of the wet weight due to Mollusca is done separately, to total wet weights of about 20 g/m^2 in May and 30 - 35 g/m^2 in September.

The two biotopes dealt with before this one, the Paraná do Xiborena and the Costa do Baixio - lotic region, were strongly dominated by flowing whitewater. The turbulence conditions at various sites in the stands were continually changing because of the continuously varying water levels, growth of the plants, removal of parts of the stand by the current etc. From a more general perspective, however, the influence of flowing whitewater did not vary significantly, so that the faunal populations existed in a sort of 'fluid equilibrium' (Fliessgleichgewicht). Under these conditions, it was reasonable to ignore the time intervals between samples and derive overall means for total abundance and biomass in those biotopes. In the shore region, however, such an equilibrium did not exist. The biocenosis was able to develop continuously through several months as the influence of currents and suspended solids gradually decreased. Our evidence indicates that the May samples represent the beginning of this development, and the September samples, its end.

Under these circumstances faunal density and biomass should not be reduced to averages over time, because insight into the course of development of the faunal community is thereby lost.

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[1] The calculation procedure is given on p. 19 f..

The following tendencies were noticed in the two preceding biotopes, which had flowing whitewater with heavy loads of suspended matter:

The Paraná do Xiborena had the highest mean current speed, lowest transparency, least faunal abundance and lowest percentage of Crustacea in the total (Table 6). In the lotic region of the Costa do Baixio, current speeds were slower, transparency was somewhat higher, and total abundance and percentage due to Crustacea were higher. This was still more pronounced in the central zone of that stand, where turbulence was further reduced by the masses of plants.

In the shore region of the Costa do Baixio, current speeds were lowest and transparency was the highest of any of these stations. Correspondingly, total abundance was at a maximum and the percentage due to Crustacea was the highest. Filter-feeders developed dense populations, especially in September. A new faunal element occurred regularly - the Conchostraca. An opposite trend was evident for the percentage of the fauna due to insects (Table 6). This percentage was highest, in the marginal region of the Paraná do Xiborena, and lowest in the central zone of the stand at the Costa do Baixio shore region.

Table 6: Percentage of mean total abundance of Crustacea and Insecta.

Station	% Crustacea	% Insecta
Paraná do Xiborena	39.9	52.3
Costa do Baixio - lotic region (marginal region)	43.6	42.9
Costa do Baixio - lotic region (central region)	61.4	28.1
Costa do Baixio - shore region (marginal region)	73.8	13.4
Costa do Baixio - shore region (central region)	80.5	11.3

The following general conclusions are drawn:

In biotopes with flowing whitewater, faunal abundance and composition is influenced predominantly by the current and its load of inorganic suspended matter. As current speeds and the load of suspended matter decrease, numbers of animals per m^2 increase, especially the filter-feeding Phyllopoda. The percentage of total abundance due to Crustacea rises, while that due to Insecta declines. No variations over large areas or of long duration could be detected in the major faunal taxa. If such variations did occur, then their expression was largely obscured by the effects of current and suspended solids.

Experiments with excelsior as a substratum

In May 1968, some field experiments were conducted to substantiate the results of the sampling studies. Two wire screen boxes, 40 cm on a side, were each filled with 150 g of excelsior (wood shavings). One box was set out on the Costa do Baixio near the shore, where the transparency was 65 cm and no significant current existed. The other was set out in the same area, but at a site with 40 cm transparency and a current speed of about 20 cm/sec. Both boxes were held at the water surface by floats, and were some 3 m from the nearest stand of *Paspalum repens.*

Total faunal abundance was much higher in the box near shore than in the one exposed to flowing water (Table 7). In the protected shore region, the fraction of total numbers due to Crustacea was about 50 %. Cladocera and Conchostraca were well represented (about 25 % of all animals!). Every one of the faunal groups included in this study was present, including the Decapoda. In contrast, abundance was very low in the lotic region. The only Crustacea present were a few Copepoda, Ostracoda and Decapoda (2 specimens) - Cladocera and the Conchostraca were completely absent. Trichoptera, Hemiptera and Odonata were each represented by a few specimens. No representatives of the remaining groups were found. Relative abundances in the two boxes confirmed the findings from studies of natural substrata.

Table 7: Experiments with excelsior as a substratum on the Costa do Baixio.

	Shore Region	Lotic Region
Copepoda	500	+
Ostracoda	1900	+
Cladocera	2000	–
Conchostraca	600	–
Decapoda	–	+
Diptera	1800	+
Ephemeroptera	2100	630
Trichoptera	100	+
Hemiptera	140	+
Odonata	+	+
Coleoptera	+	–
Hydracarina	+	–
Oligochaeta	800	–
Mollusca	270	–
Total Abundance	10210	630

However, the numbers of animals on the excelsior were small relative to those on natural substrata, even in the shore region. When the data are transformed to numbers per m^2, it is evident that the boxes sustained only 50 % of the faunal density which was established on the vegetation. This means that, under the existing environmental conditions, either the excelsior was not as good a substratum for the animals as the vegetation, or those animals living in the boxes did not have as large a supply of food. Further experiments with the same substratal material in Lago Calado revealed that the abundance of fauna on the excelsior depends primarily on the amount of edible material (detritus and phytoplankton) carried into the boxes by the current, and probably to a lesser extent on the growth of microbes on this substratum, as well (see substratum experiment in Lago Calado, p. 49 ff.). In consideration of this fact, it may be assumed that when the excelsior was sampled, the available food (i.e., phytoplankton and organic detritus) was less there than in the vegetation. The relationship between phytoplankton production, current and amount of inorganic suspended solids has already been discussed.

Besides illustrating the importance of currents to the fauna, this experiment also shows that the floating vegetation in flowing whitewater serves the animals both as substratum and as a fundamentally important factor in their food supply.

3. Lago Calado

Description of the biotope:

Lago Calado, a typical várzea lake, lies about 10 km below Manacapurú on the left bank of the Solimões (fig. 2). The lake basin is divided into various bays. A tributary rivulet drains the terra firme and adds electrolyte-poor water. A connection with the Solimões persists, even at low water levels. At those times, most of the bottom of the lake dries up. Only in the center is there a shallow pool of residual water which is very turbid (transparency about 20 cm) as a result of wind induced turbulence. No stands of floating vegetation are present then. As water levels rise, the residual water is pushed back and diluted to some extent by inflowing water from the Solimões.Simultaneously, the onset of the rainy season causes increased runoff fromthe terra firme into the lake. As a result, the chemistry of the water changes considerably from the junction between lake and river back up into distant inlets. The differences develop to different extents from year to year, since they are very sensitive to the rate of rise of the Solimões and to local precipitation conditions.

Station 1 - Upper end of the lake

Station 1 lay in a deeply indented inlet, well protected from the wind. At low water, the exposed bottom of the innermost part of this inlet was covered with stands of vegetation several hundred meters in extent, mainly composed of *Echinochloa polystachya* and *Paspalum fasciculatum*. Scattered patches of the terrestrial form of *Paspalum repens* occurred in the outer part of the inlet. The entire area was drained by a small rivulet arising in the terra firme. Part of the exposed lake bottom was planted with jute (*Corchorus capsularis)* during low water levels. As the water rose, a distinct zonation of the vegetation was formed. The outer edge, which extended farthest into the lake, consisted of a flourishing belt of *Oryza perennis*, mixed with *Panicum chloroticum*. Behind this was a band of *Paspalum repens*, while the entire upper portion of the inlet was covered with *Echinochloa polystachya* and *Paspalum fasciculatum*. At higher water levels, *Panicum chloroticum, Paspalum fasciculatum* and *Oryza perennis* disappeared. In February, there was a heavy bloom of *Azolla spec.*and *Salvinia auriculata*. Beginning in March, *Neptunia oleracea* appeared in somewhat greater abundance. For a long time, the *Paspalum repens* stand remained relatively sparse, so that a distinction between marginal and central zones on the basis of their biotopic characteristics was impossible until July.

Physical-chemical investigations:

The color of the water in this part of the lake was at no time influenced by influxes of sediment-rich whitewater. The water was transparent, and at the beginning of the year, had a deep reddish-brown color. During the following months it graded over into olive or brownish. Also, transparency increased to more than 2 m (fig. 11). The very low transparency of 40 cm in December was due less to the influence of the rivulet flowing from the terra firme than to high levels of humic materials, dissolved by the rising water from organic matter that had decomposed during the dry season.

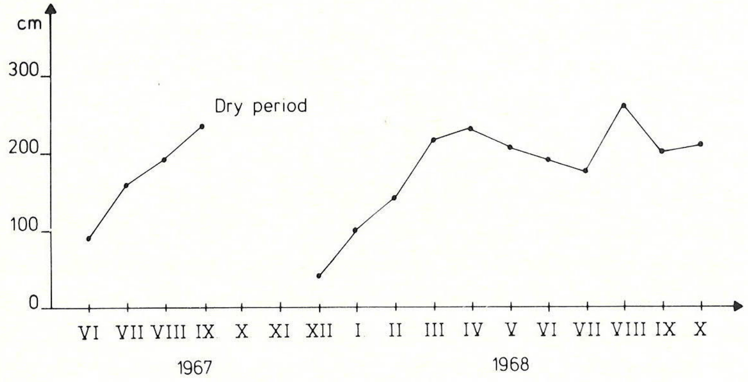

Fig.11: Lago Calado (upper end of the lake) Visibility in the course of the year

Conductivities reached a maximum in December as a result of the action of the 'shore factor' (fig. 12). In January, they decreased steeply (dilution with electrolyte-poor water from the terra firme), then began to rise again slowly until June. The latter increase may be traced to a weak influence of 'sedimented' Solimões water. In 1968, this exchange of water was not nearly so extensive as in the preceding year. In July, the influences from the terra firme were able to re-assert dominance, for water levels had already begun to recede. Conductivities then remained very low until the inlet dried up. Values of pH, which lay between 5.4 and 6.4 during the 1968 investigative period, also decreased considerably in July (fig. 12).

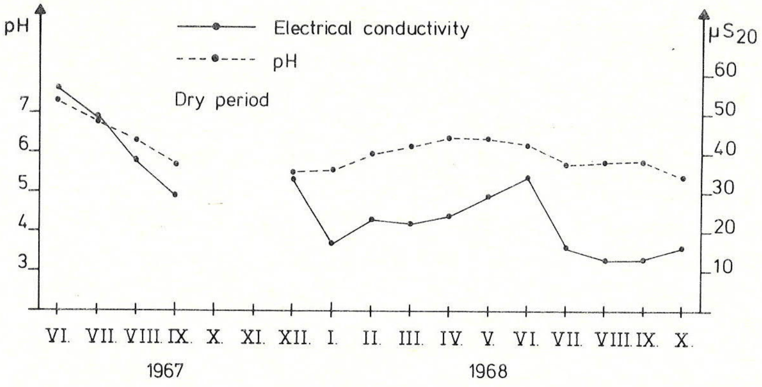

Fig.12: Lago Calado (upper end of the lake): pH-value and electrical conductivity in the course of the year

In September 1968, dissolved oxygen levels were significantly higher at sunset than at sunrise in the open water, because of the assimilatory activities of the phytoplankton. Deeper than 150 cm, oxygen concentrations remained low and varied little (fig. 13 a). In the band of *Paspalum repens,* a distinct horizontal stratification of dissolved oxygen was established. This was because of the structure of the stand, and may be considered characteristic for all such stands of plants (fig. 13 a). Values were highest in the uppermost layers, then dropped immediately to a minimum, finally rising again to form a secondary maximum. The secondary maximum was rather weakly formed in this case. The first maximum lies in the euphotic zone and is predominantly due to the photosynthetic activity of the algae there. The secondary maximum arises through horizontal exchange between the open water beyond the vegetation and the water beneath the cover of plants. Beneath the densest parts of the vegetation, exchange of water is poorest, the influence of the two oxygenating factors is weakest, and oxygen consumption is greatest. Depending on the density of growth in the stands, the minimum oxygen concentration can occur at varying depths, e. g., at 10 or at 30 cm. The weakly formed secondary maximum ends at a depth of 1 m in this case; at that level, the oxygen concentrations are equal to those in open water at night. Since it may be assumed that the water mass beneath the plant cover is largely sheltered from weak turbulence, this fact leads to the deduction that a rather stable stratification of the entire water mass in this inlet existed at the time of measurement. Furthermore, it is evident that extensive oxygen depletion can occur under the grassy cover, especially when calm weather or the morphology of the lake prevents adequate horizontal exchange with the surrounding, oxygenated water (see p. 81).

the difference in temperature of the water between the surface and a depth of 150 cm was still 3.0° C at 17:30 h. Table 8 shows that this stratification was first established in the daytime, reached a maximum as the sun's rays penetrated most strongly in the early afternoon (34.5°C surface temperature!), then largely disappeared again during the night. The sharpness of the stratification depends on the weather, and can be entirely prevented by wind action. BRAUN (1952) obtained the same results in his investigations of the lakes along the

lower reaches of the Rio Tapajós. He found a temperature difference of 1.7°C in the region of the thermocline. RUTTNER (1931) similarly determined that a temperature interval of 1.25°C existed in the region of the thermocline in 5 - 10 m depths in Ranu Lamongan, a crater lake on Java. In calm weather, the average temperature difference in the inlet between the surface and 25 cm depth was 1.6°C during the early afternoon.

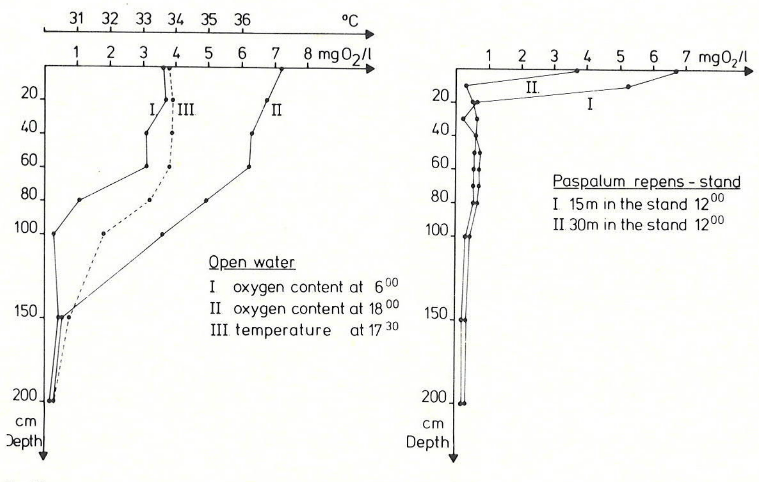

Fig 13a

Fig 13b

Fig 13a,b Lago Calado (upper end of the lake): oxygen content and temperature (8.9.1968)

The particularly high temperatures and temperature differences in this inlet of Lago Calado were due to the wind-sheltered location and a strip of floating vegetation about 5 - 20 m wide which protected the inlet against waves from the lake.

Within the stand, the surface temperature rose as high as 40°C, for circulation of the water was hindered by the mesh of plant tissues (Table 8). Such a high temperature still would not have occurred, however, if the stand had not been in a senescent condition, in which shading of the water by leaves and sprouts was severely reduced. RUTTNER (1931) reports a maximum water surface temperature of 39.7°C for a dense, partly submerged stand of *Hydrilla* in Ranu Lamongan.

The faunal community:

Figures for total abundance are marked by the occasionally high faunal densities. After a slow increase which began in December, one maximum was reached in April, then a second in July (fig. 14 a). When abundance is broken down into faunal groups, it becomes evident that these maxima are mainly caused by fluctuations in the most numerous group, the Cladocera (fig. 14 e). Copepoda had high numbers of individuals in April and July, also. Ostracoda, in contrast, showed no maximum in April, but did have one in June and July. Conchostraca were present throughout the year, attained a small maximum in April, but proliferated most in July. Also, considerable quantities of this animal were

Table 8 : Temperature fluctuations in the course of a day (6.9.1968, Lago Calado).

Depth	Time	Open water	Margin of the Stand	Within the Stand
0 cm		30.3° C	30.5° C	30.5° C
10	6^{00}	30.3	30.5	30.7
40		30.3	30.5	30.7
0 cm		33.5	37.0	38.0
10	12^{00}	33.5	34.0	38.0
40		33.5	33.5	31.3
0 cm		34.5	37.5	40.0
10	14^{30}	34.5	35.5	38.5
40		34.5	34.5	34.0
0 cm		33.8	33.9	35.2
10	17^{30}	33.8	33.9	35.0
40		33.8	33.8	34.0

still present just before the plants were stranded by sinking water levels. The pattern of abundance for Insecta was again mainly due to the most abundant group, the Diptera. These, too, showed maxima in April and July, but had still another before the inlet dried up. Trichoptera were most numerous in July, but Ephemeroptera never developed a distinct maximum abundance (fig. 14, c - i).

If the total abundance in the peripheral zone is compared with that of the central zone of the stand, it is evident that the fauna as a whole was about equally numerous or slightly less so in the central zone. The same was true for the separate taxa, with the exceptions of the Trichoptera and the Ephemeroptera. For these, there was generally a decided decrease in abundance from the periphery toward the center of the stands. The one instance in which this did not hold true was a sample taken in July, 1968; Ephemeroptera were more abundant in the center. In this case, a small (about 1 m^2) open surface of water occurred in the stand near the location of the sample, and these animals may have been more abundant around its edges.

It was clear, moreover, that replicate samples from Lago Calado, too varied substantially in total abundance and faunal composition. For example, the three samples taken at 10 m intervals in April show quantitatively and qualitatively different populations of Cladocera in each case. In two samples, the dominant form was a species of the family Daphniidae, while Chydoridae was the most abundantly represented family in the third one.

Fig. 14 a - i: The aquatic fauna in the floating vegetation of Lago Calado (upper end of the lake) in the course of the year.

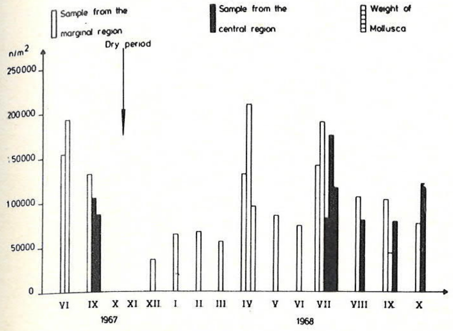

Fig.14a: Total number of individuals

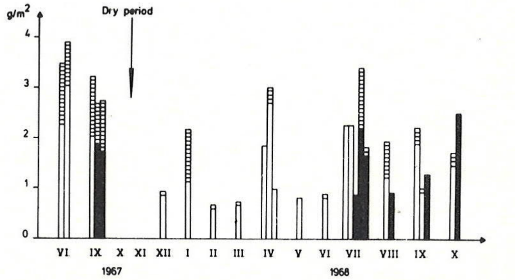

Fig.14b: Total dry weight (without large individuals)

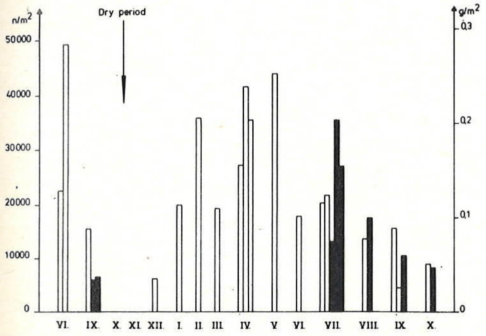

Fig.14c: Copepoda

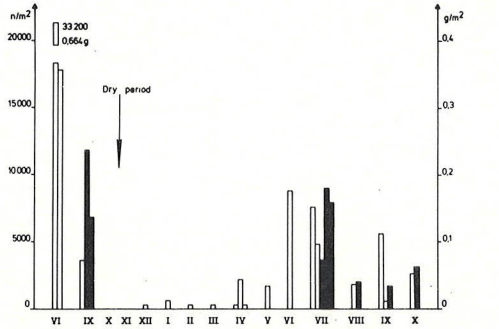

Fig.14d: Ostracoda

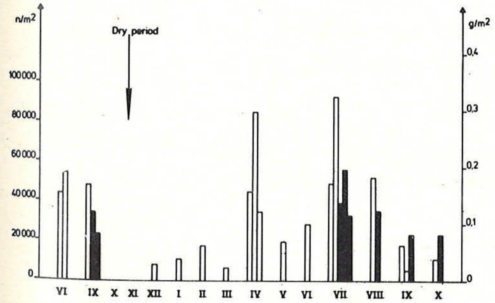

Fig.14e: Cladocera

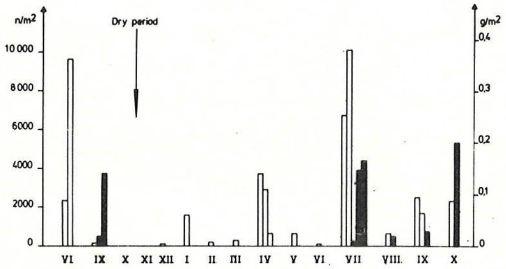

Fig.14f: Conchostraca

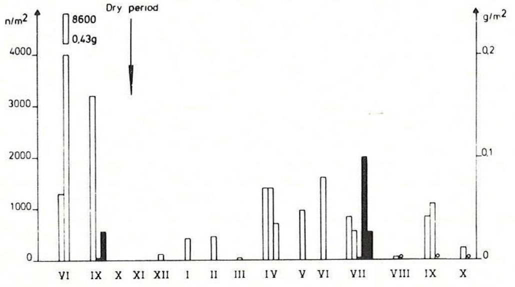

Fig.14g: Ephemeroptera

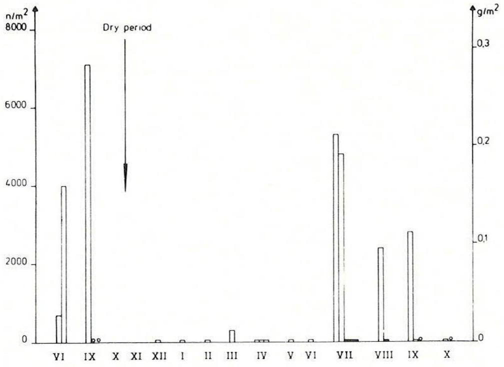

Fig.14h: Trichoptera

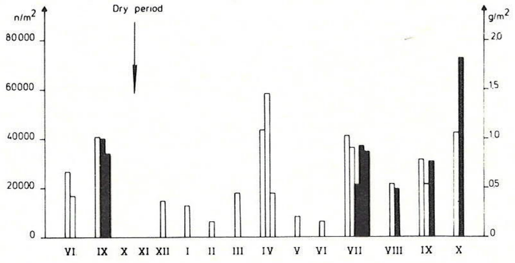

Fig.14i: Diptera

As on the Costa do Baixio, no decisive dependence of abundance on the root mass could be found in Lago Calado. Only when the root mass was very small was there ever a distinctly related decrease in numbers of animals. Rather, it should be stressed that even such a small area as that included in a sample is strongly influenced by factors whose significance and variety are as yet unknown. Examples of such locally-acting factors are incident radiation, relationship to the immediate surroundings, age and distribution of the substratum, algal biomass, aggregations of animals etc. The quantity of roots would seem to become limiting only in exceptional cases.

In view of this faunal heterogeneity, the reality of the previously described maxima and minima may appear doubtful. However, the patterns have been substantiated by experiments with artificial substrata, as will be shown in the following section.

The samples from June and September, 1967 show that abundances were also high in the preceding year. It is of particular interest that total abundance was still very high just before the plants were stranded. When faunal groups were tallied separately, it was determined that in both years Cladocera, Copepoda and Ostracoda decreased, but Diptera increased, near the end of the year. More detailed discussion of these findings will follow a description of the other investigations in Lago Calado.

Total biomass had basically the same pattern of maxima in April and July as that for total abundance, but the July maximum was not so marked in this case (fig. 14 b). In addition, the January sample had a relatively high dry weight in relation to the number of animals, because of the high proportion of Mollusca. Diptera regularly constituted a significant fraction of the weights shown. The maximum dry weight for this group was 1.82 g/m^2 (October 1968). This is equivalent to a wet weight of about 13 g/m^2. Here again, the average weight of the pre-sorted, larger animals must be added to the figures for dry weight. This weight was 2.22 g[1].

The corrected total biomass at this station varied between 2.9 and 6.1 g dry weight per m^2. This corresponds to a wet weight of about 14 - 30 g/m^2 when the contribution of Mollusca is calculated separately.

Experiments with excelsior as a substratum

The importance of the floating vegetation for the aquatic fauna was tested here, as on the Costa do Baixio, by means of wire boxes 40 cm on a side with mesh openings of 1.5 x 2 cm. These were filled with 150 g of excelsior each (photo 3) and set out near the stand of *Paspalum repens*. Excelsior, (wood shavings) was chosen because on one hand, it is a natural substratum, while on the other, its inherent food value for the investigated groups is negligible. The boxes were left out for one month, at the end of which there was no macroscopic evidence of any significant alteration of the material.

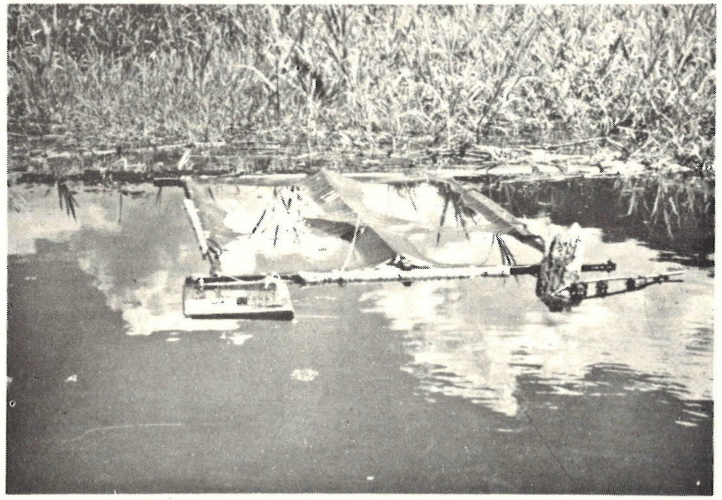

Photo 3 : Experimental set up near the *Paspalum repens* stand in Lago Calado.
Light and dark boxes with excelsior as substratum.

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[1] See p. 19 f. for derivation of this value.

This experimental approach was assumed to provide the same environmental conditions of light, temperature, turbulence, oxygen concentration, available food etc. which occur in the peripheral zone of the floating vegetation. After one month, a large amount of voluminous, reddish-brown detritus, which was similar to that in the surrounding root masses, had collected in the interstices of the excelsior. This detritus contained 58 % volatile solids. The residue consisted of diatom tests and $Fe(OH)_3$ precipitate. Moreover, large quantities of Chlorophyceae were found inside the boxes.

Faunal abundances were very great (fig. 15 a). The pattern illustrated by the histogram confirmed the reality of the April and July maxima seen in samples from the floating vegetation. We are confident, therefore, that these were genuine fluctuations of faunal abundances in this part of the inlet, and not merely artifacts due to the natural, small-scale variations in abundance described above.

Separate consideration of the abundances of each of the major taxonomic groups also confirms the results of the sampling studies in the floating vegetation. Again, the Ephemeroptera were irregular in abundance, but showed a distinct maximum in July on the excelsior, as they did on the roots (fig. 15, e - h).

One to three larger fishes (*Cichlasoma severum* HECKEL, *C. festivum* HECKEL, and *C. bimaculatum* LINNE [Family Cichlidae] and snails (*Ampullarius spec.* [Family Pilidae], were regularly found inside the boxes. These had penetrated the wire meshes, then grown so large that they were unable to get out.

The first faunal maximum, in April, is not so clearly expressed in the graph of biomass (fig. 15 b), since it was mainly due to the Cladocera. Individuals in this group contributed much less to the total biomass than specimens of the Conchostraca, which were extremely abundant at the time of the second maximum of total abundance in July. Each experimental box yielded biomass values (excluding the larger animals removed prior to subsampling) of about 0.2 g dry weight during the faunal minima, and climbed to about 2 g on the average at the time of the July maximum. On a common basis of a square meter, both abundances and biomasses in the excelsior-filled boxes were as large as, or even greater than those in the floating vegetation during peak periods. It was especially striking that the proportion of both numbers and biomass of the fauna which was due to Crustacea in the interstices of the excelsior was considerably higher than among the roots of the vegetation.

It is demonstrated by this experiment that, at least sometimes, a substratal material which may be considered to have very little nutritional value to the animals can be densely populated by them. This result also implies that the floating vegetation, in at least some instances, serves primarily as a substratum for the community and plays only a subordinate role in its nutrition.

However, it is also conceivable that in these experiments only the close proximity of the vegetation enabled such a successful faunal development in the boxes, and that the ecological conditions in the excelsior would have been less advantageous without the direct or indirect influence of the vegetation. Furthermore, questions arise concern-

Fig. 15a - i: The aquatic fauna in the sample boxes with excelsior as substratum in Lago Calado (upper end of the lake).

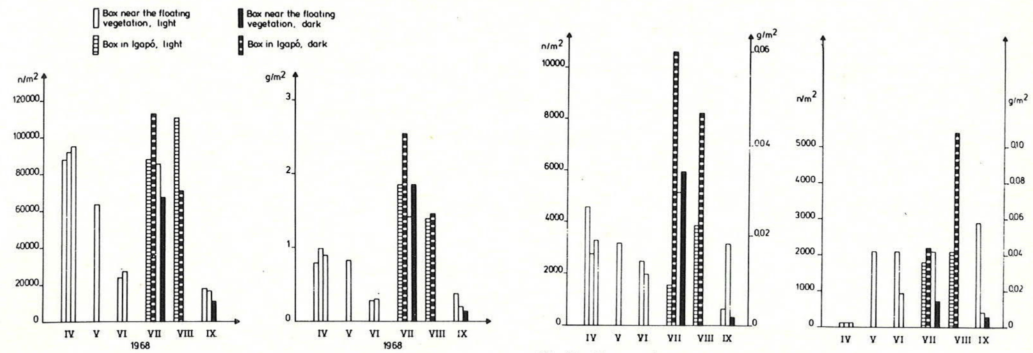

Fig.15a: Total number of individuals

Fig.15b: Total dry weight (without large individuals)

Fig.15c: Copepoda

Fig.15d: Ostracoda

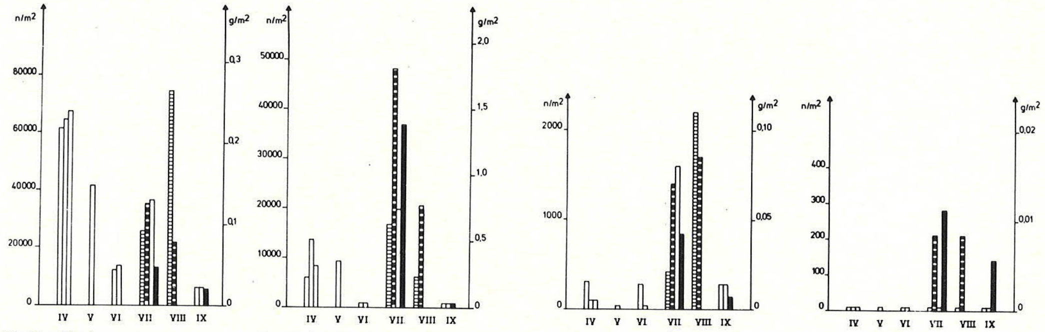

Fig.15e: Cladocera

Fig.15f: Conchostraca

Fig.15g: Ephemeroptera

Fig.15h: Trichoptera

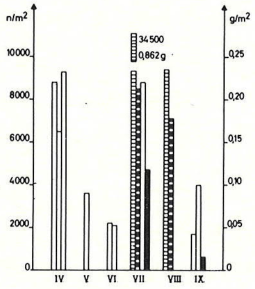

Fig.15i: Diptera

ing the identity of the primary source of food for the community, and the significance of the Chlorophyceae, which develop in the boxes under favourable light conditions, as source of energy for the fauna.

To answer these questions, four identical boxes were set out among submerged bushes about 150 m from the nearest floating vegetation (photo 4). A ring of submerged bushes prevented any floating islands from drifting nearer to the boxes than 50 m on any side. Two of the boxes were shaded with a floating black cover 2 m x 2 m in size to block out incident light without interfering with circulation of the water around and through the boxes. Two other boxes shaded in this manner were set out beside the exposed boxes on the periphery of the floating vegetation (photo 3).

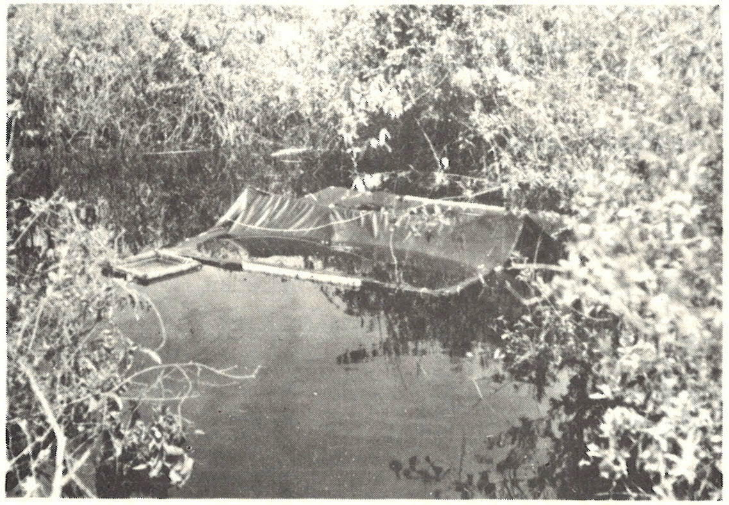

Photo 4 : Experimental set up in flooded várzea forest of Lago Calado. Light and dark boxes with excelsior as substratum.

In July, the animals in two of the boxes set near the vegetation and two which had been set away from it were examined. One of these boxes from each location had been shaded. All boxes contained large amounts of voluminous, brown detritus, but the quantity in the shaded boxes was significantly less. The abundance of animals was not increased by proximity to the floating vegetation; on the contrary, numbers in the boxes set well away from the meadow were a little higher than in those near it. The water level then began to fall, so the remaining two boxes which had been set out among the submerged bushes had to be removed and examined only two weeks later. They showed similar high faunal abundances (fig. 15 a - h).

It is more difficult to evaluate the relative effects of shading versus exposure on faunal abundances in the boxes, for on one hand, the differences were not consistent in all four pairs of experimental boxes; and on the other, it is possible that the experimental procedure had some influence of its own on the biocenoses.

In three cases, the total number of animals was lower in the shaded boxes. It is not possible to conclude unequivocably from this that threre was less food available in the shaded boxes, as would be expected to result from a reduction in the sessile algae, because different kinds of animals showed contradictory patterns of response. Copepoda and Conchostraca were each more abundant in three cases in the shaded boxes, but Cladocera and Ephemeroptera were more numerous in boxes exposed to the light in three of the sets. Ostracoda were more numerous in the light-exposed substrated material near the meadows, but seemed to prefer the shaded boxes among the submerged bushes. Only Diptera preferred the light-exposed boxes in all four sets, while the usually rare Trichoptera were consistently more abundant in the shaded ones.

Several aspects of the experimental approach should be considered as sources of differences, in addition to environmental factors. First of all, the shading was not complete, since only that light coming from directly above was excluded. Any other shading arrangement, kowever, would have interfered with circulation of water around the boxes, and hence colonization-by animals from surrounding biotopes. In this regard, it is still possible that colonization by means of eggs laid by Insecta on the surface of the water was hindered by the covers, and this would explain the consistently lower abundances of Diptera in the shaded boxes. It is further possible that some kinds of animals could be using the shaded boxes only during the day as a refuge from the sunlight. Other such temporary utilization of the boxes is also conceivable. For these reasons, a more detailed interpretation of the experimental results will not be attempted.

These experiments nevertheless provide some general evidence for the feeding habitats of the fauna. The large numbers of sessile forms (especially Conchostraca) show that a sufficient source of food was available to these animals in all the boxes. Since excelsior is essentially valueless as food for the taxa investigated here, the principal source of nutrition must have been the brown, voluminous material. It consisted largely of detritus, phytoplankton and $Fe(OH)_3$. Most of the plants growing on the excelsior were restricted to the outer surfaces by the shading, and could not have contributed significantly to the quantity of available food, anyway. Sessile Chlorophyceae were not macroscopically evident in these boxes, but they were consistently visible in experimental boxes exposed to the light. Phytoplankton and detritus trapped in the substratum, whether it was excelsior or roots, from water moved past it by wind or thermal currents seemed to be much more important as food sources.

As oxygen concentrations show (fig. 13 b), exchange of water is greatly reduced only a few meters into the central part of the vegetation. This indicates that the provision of phytoplankton to the animals living in this zone was also much less. The relatively small amounts of detritus trapped among the roots in the inner parts of the stands also support this inference. Autochthonous algal production is limited to a layer of water just a few centimeters thick which lies above the intermeshed mass of roots and rhizomes. Below this layer, there is so little light that algal primary production is virtually eliminated. This deprives the animals of most of their food base.

Samples from the inner parts of the stands, however, show that high faunal abundances occur here, too. It must therefore be assumed that the animals present in this zone utilize the floating vegetation itself, at least partially, as food. Either the dead plant remains are eaten directly, or bacteria which are associated with the decomposition of old rhizomes and leaves serve as an energy source for, e. g., the Cladocera which occur in great abundance there. In this case, the floating vegetation is both substratum and food for the animals living on it (DIONI 1967).

From this it can be deduced that faunal fluctuations should be less extreme in the vegetation than in the experimental boxes. The most probable cause of the observed fluctuations, which occurred more or less synchronously in almost all the faunal groups, was the fluctuating supply of phytoplankton and other sources of food. Fauna in the vegetation, however, can use the plants themselves as a supplementary food source, and fluctuations in their abundance were clearly less extreme. The broadest fluctuations occurred in the boxes of the artificial substratum, excelsior, because the animals growing in them depended almost entirely on material from the surrounding water for food.

Another train of events also seems to fit in with this explanation of faunal fluctuations. Oxygen and temperature values in September showed a well-developed stratification of this part of the lake (see p. 45). Sedimentation of dead plankton into the hypolimnion which existed at that time may have impoverished the surface layers, and through this, affected primary production and the fauna.

These problems, however, are beyond consideration in the present studies, for they require a larger number of samples and more detailed investigations of primary production, species composition of the fauna and nutritional requirements of individual species for proper study.

Station 2-lake outlet

Physical-chemical investigations:

The second station in this lake lay near its outflow, some 500 m from the connection with the river. During the period of rising water levels, this area was alternately under the influence of slowly flowing, relatively clear ('decanted') lake water and inflowing whitewater, which was rich in suspended solids. Reversal of the flow depended on the rise of the Solimões and local rainfall, and occurred irregularly but rather frequently. The apparent monthly periodicity of flow reversal indicated by transparency (fig. 16) is deceptive in this respect. Changes in the color of the water showed that several could occur within a few days. The current was very slow. As at station 1, pH decreased towards the end of the year, presumably because of the influence of water draining from the terra firme. The low conductivities of water flowing out of the lake indicate that in 1968, the influence of electrolyte-rich water from the Amazon was relatively weak,

and the chemistry of the lake was strongly dependent on rainwater and tributaries from the terra firme (fig. 17). The temperature of the surface water varied between about 30°C and 33°C.

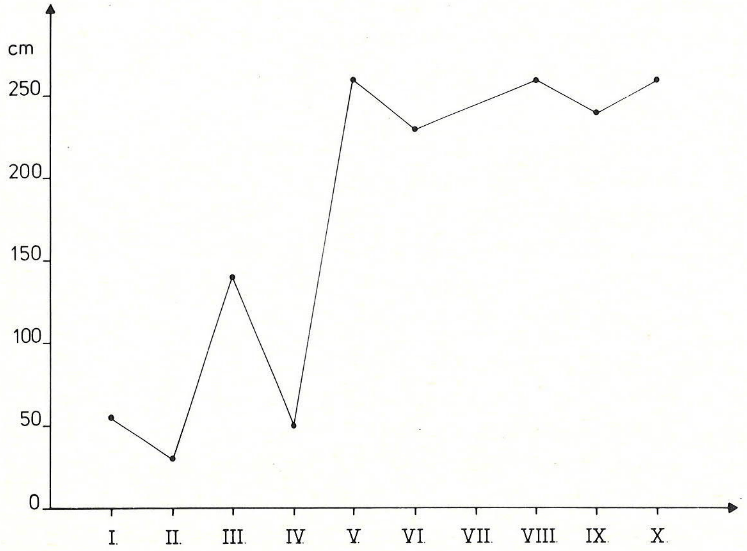

Fig.16: Lago Calado (lake outlet): Visibility in the course of the year

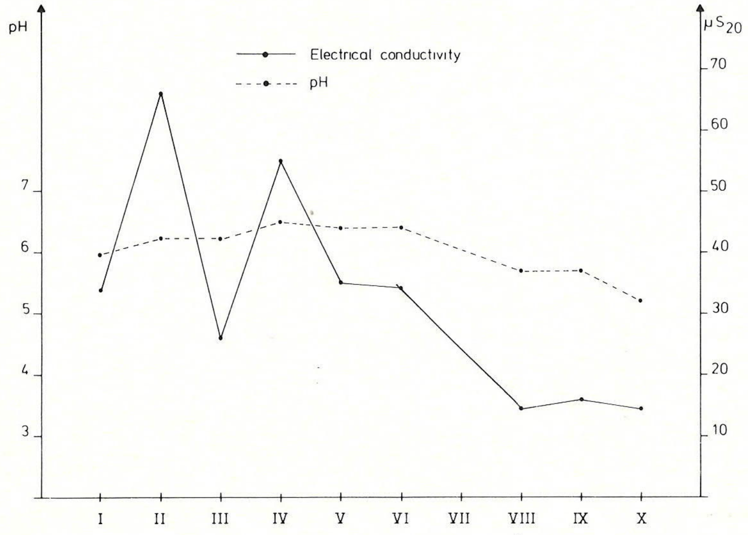

Fig 17 Lago Calado (lake outlet) pH-value and electrical conductivity in the course of the year

The faunal community:

Total abundances present quite a different pattern from that at station 1 (fig. 18 a). At this site, the numbers of animals were initially low, then increased steadily until the end. The one pronounced maximum occurred in September/October, just before the area dried up. Separate faunal groups showed no greater similarity to station 1 (fig. 18, c - i). Only Diptera exhibited some parallel changes at the two stations. Conchostraca were present for the entire period, and in large numbers from March on. The maximum for each of the faunal groups fell in September or October.

Biomass showed about the same pattern as abundance (fig. 18 b). The proportion of dry weight due to Diptera was less than in the inlet, but these and Mollusca were again the most important groups. The minimum weight at the beginning of the year, including the averaged weight of the larger, pre-sorted animals (2.22 g[1]),was about 2.5 g/m^2, and the maximum was about 5.5 g/m^2. These correspond to wet weights of about 12 and 28 g/m^2, respectively, when the molluscan portion is calculated separately.

At the inlet station in Lago Calado, only Diptera and Conchostraca showed any increase in abundance near the end of the year, while all other groups decreased. At the station near the outlet, the abundances of all groups continued to increase until the stand dried up. Thus, the decline in numbers of individuals in the inlet cannot be assumed to indicate an adaptation of the fauna to the periodical dry season. Rather, the most obvious explanation for the differing patterns of faunal development at the two stations is the difference in food supplies.

Fig. 18a - i: The aquatic fauna in the floating vegetation of Lago Calado
(lake outlet) in the course of the year.

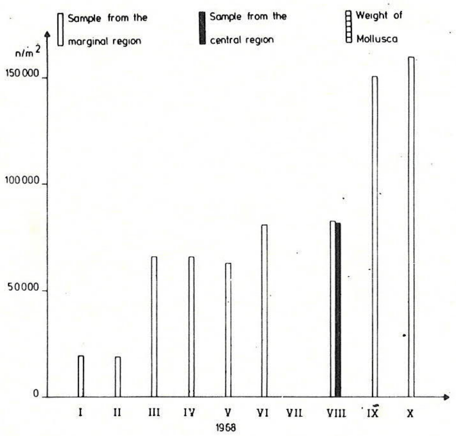

Fig.18a: Total number of individuals

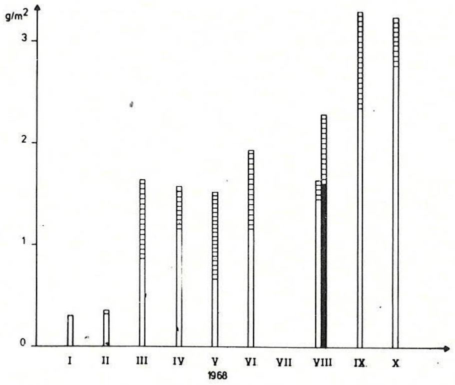

Fig.18b: Total dry weight (without large individuals)

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[1] See p. 19 f. for calculation of this value.

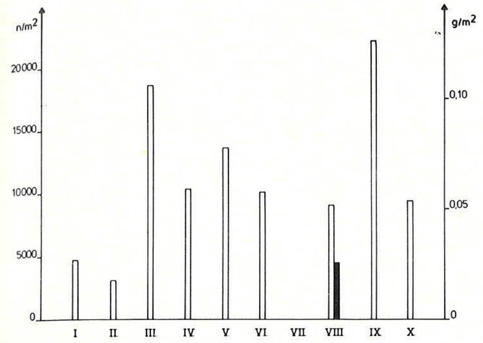

Fig.18c: Copepoda

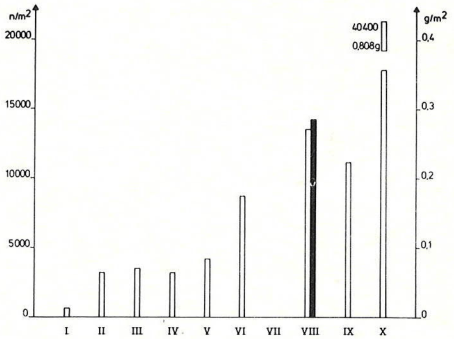

Fig.18d: Ostracoda

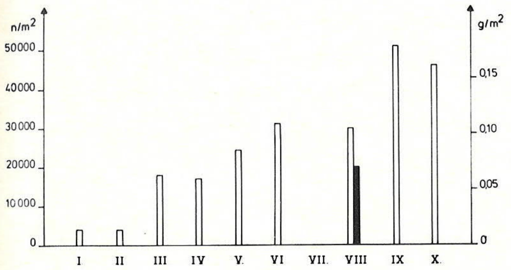

Fig.18e: Cladocera

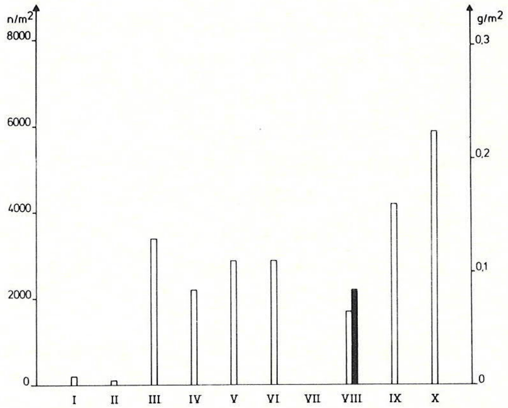

Fig.18f: Conchostraca

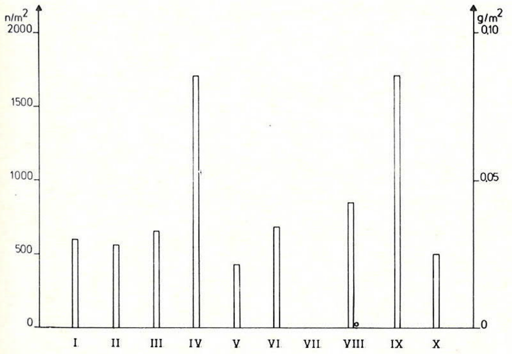

Fig.18g: Ephemeroptera

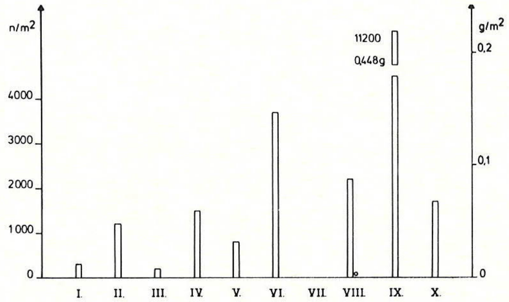

Fig.18h: Trichoptera

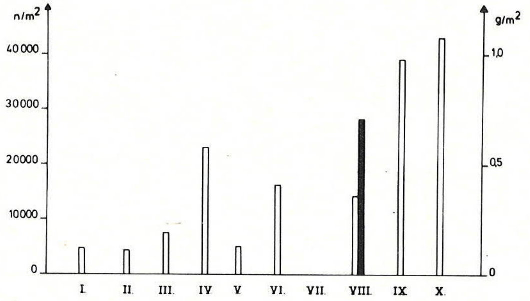

Fig.18i: Diptera

The relatively low faunal densities in the outlet area were caused by the influence of whitewater from the Solimões, which continued to flow in until May. It had no effect on the remote inlet, and the fauna therefore reached a maximum as early as April. After June, the water level began to fall gradually. The whitewater effect ceased and abundance slowly increased near the lake outlet. Toward the end of the year, a very stable stratification developed back in the inlet in Lago Calado, because of its protection from the wind. Temperature and oxygen data provide ample evidence of this. The stratification apparently led to an impoverishment of the surface layers when dead phytoplankton sank into the temporary hypolimnion and its remineralization products were retained there. Presumably, this was followed by a decline in phytoplankton production and with it, the food supply of the animals. The net effect was a reduction in faunal abundance. Abundances of animals were especially affected in the excelsior, for phytoplanktonic production was practically the only source of energy in that substratum.

Such stratification could not develop near the lake's outlet, for a weak current was maintained after September as water levels declined. This current continually added fresh phytoplankton and detritus to that among the roots, so the food base there increased steadily. The result was continual growth of the faunal community until the stand dried up. This explanation is supported by the results of studies in Lago Manacapurú, where a similar mechanism was much more clearly at work (see p. 64 ff.).

In summary, the following points about the fauna of the floating vegetation in Lago Calado have been established:

The floating stands which develop as water levels rise are immediately colonized by aquatic animals. These animals reproduce rapidly. In spite of this multiplication, the numbers of individuals per m^2 were relatively low at first due to the explosive growth of the vegetation in the early months. Variability in abundance and species composition within a small area was very great. This situation probably resulted from multiple factors, including incident light, structure of the local surroundings, distribution and density of the substratum, aggregations of animals etc. No clear dependence of abundance on the amount of roots per m^2 could be found. Only in very sparse root mats did the fauna obviously decrease. No general factor could be isolated which exerted a fundamental effect on the fauna throughout the lake, as current and concentration of suspended solids do, for example, in the whitewater biotope. Thus it was possible for the aquatic fauna to develop differently in different parts of the same lake. Oxygen concentrations in the central zone of the *Paspalum repens* stands were much lower than in the peripheral zone. Yet this difference seemed to have no great effect on total abundance, perhaps because the fauna in the narrow layer which was lowest in oxygen could escape this extreme condition by moving upwards or downwards into better oxygenated layers.

The average number of individuals per m^2 over all samples from the peripheral zone was slightly higher than that for all samples from the central zones of the stands. Because of large local variations among single samples, the opposite trend of abundance could have existed. Trichoptera and Ephemeroptera exhibited definite decreases in abundance from the periphery inwards. Conchostraca were regularly present in both zones of the stands, sometimes in very large numbers. Mean total abundance was higher than in those biotopes which were predominantly influenced by flowing whitewater. The same was true for total biomass. Insecta accounted for a significantly larger fraction of the total dry weight than the Crustacea in the stands which were investigated. In the experiments with excelsior as a substratal material, however, Crustacea were dominant. On the margins of the stands, phytoplankton which was carried into root masses by the turbulence of the water was very important to the fauna, as the experiments with excelsior showed. In this zone, the floating vegetation mainly filled the role of substratum for the community. In the inner parts of the stands, the detritus which fell from the vegetation itself was presumably the main source of food, whether directly as particulate organic matter or indirectly through the bacteria and other microbiota it supported.

The different sections of the lake exhibited large quantitative fluctuations in individual species and total abundances independent of one another. The causal factors of the fluctuations could not be precisely determined. Variations in the water chemistry of the lake probably played an especially important role[1] by its influence on the phytoplankton, and hence the food supply of the animals.

4. Lago Manacapurú

Description of the biotope:

Lago Manacapurú empties into the Solimões about 80 km above its junction with the Rio Negro near the town of Manacapurú. It is the core of a large system of lakes with many islands which develops during high water levels and extend far back into the terra firme. A large influx of water is carried by the Rio Manacapurú from the terra firme, so most of the lakes are blackwater lakes (see fig 2, p. 22). There is normally a flow out of the lake into the Solimões throughout the year. This lake system may therefore be viewed partially as the drowned valley of the Rio Manacapurú. Whitewater from the Solimões, however, penetrates into this lake system by way of Lago Cabaliana, upstream of the normal outlet. The extent to which this whitewater mixes with the blackwater in the lakes depends on hydrographic conditions at the time of its penetration. Penetration of whitewater behind the leveé enables a várzea-type vegetation to exist there.

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[1] GESSNER (1955) pointed out that differences in surface temperatures lead to a mosaic of differently stratified water masses within tropical lakes.

The sampling station was 3 km from the outlet near a low, shrub-covered island which was flooded during high water levels. A stand of *Paspalum repens* with some *Echinochloa polystachya* several hectares in extent developed in the crowns of the shrubs as water levels rose. At maximum water level, large portions of the stands not anchored firmly to the submerged bushes were carried off by the current. In November and December, the station was dry land, inhabited by terrestrial grasses. These were drowned by the rising waters, and accumulated in rotting masses in locations protected from the currents and among the branches of the bushes.

Physical-chemical investigations:

In this section of the lake there was a continuous, outward flow to the Solimões, interrupted only briefly at the early stages of rising water levels. After the first three months, the water became brown or deep, reddish brown in color, and the transparency was not influenced by whitewater after March (fig. 19). The high conductivities in December and January are attributable to both the influence of the invading, electrolyte-rich whitewater and to the "shore factor". Thereafter, influence of the electrolyte-poor, acidic blackwater from the Lago Manacapurú became increasingly strong, as evidenced by rapidly declining conductivity and pH (fig. 20). At maximum high water in April and May, conductivity had dropped below 10 μS_{20}, and pH to 5.3. These values are essentially the same as for pure blackwater, except for the slightly higher pH. As the waters receded, electrolyte-rich water draining from Lago Cabaliana sometimes replaced the blackwater of Lago Manacapurú. Conductivities and pH's increased, but very irregularly, because water levels in the Solimões receded irregularly. The water levels in the river controlled the relative influence of the two water masses in the lake. Declining values in July illustrate this irregularity, but such reversals must have occurred more often than the monthly measurements show. The electrolyte-rich water, in this case, carried no suspended solids and did not differ much in color, so that only pH and conductivity gave evidence of its physical-chemical influence. Its biological effects will be discussed below. A similar pattern of changes between May and August of 1967 shows that they recur annually with only minor variations. This occasional influence of water richer in electrolytes is clearly sufficient to substain a healthy stand of *Paspalum repens* and *Echinochloa polystachya*, as well as *Pistia, Eichhornia, Salvinia, Marsilia* etc. Slow currents have a favorable effect on the stands in that they maintain circulation of the water into the central zones. Even at the end of the vegetative period, when the vegetation in standing waters of other lakes is showing clear signs of senescence, only the barest indications of impending changes, such as rotting, formation of thinner, tougher sprouts etc. are evident among the *Paspalum repens* in Lago Manacapurú.

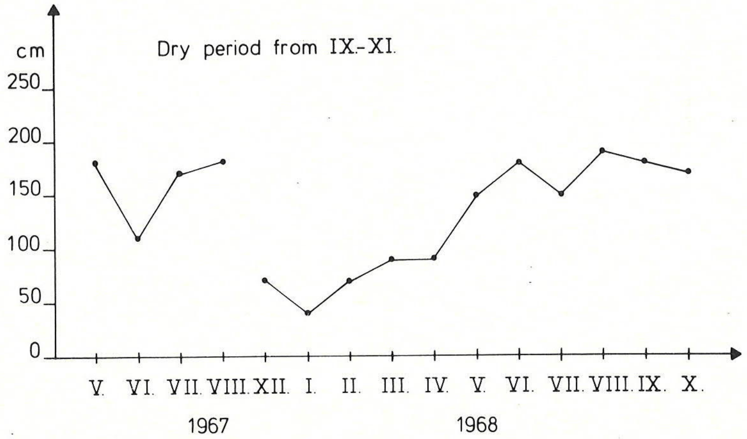

Fig.19: Lago Manacapurú: Visibility in the course of the year

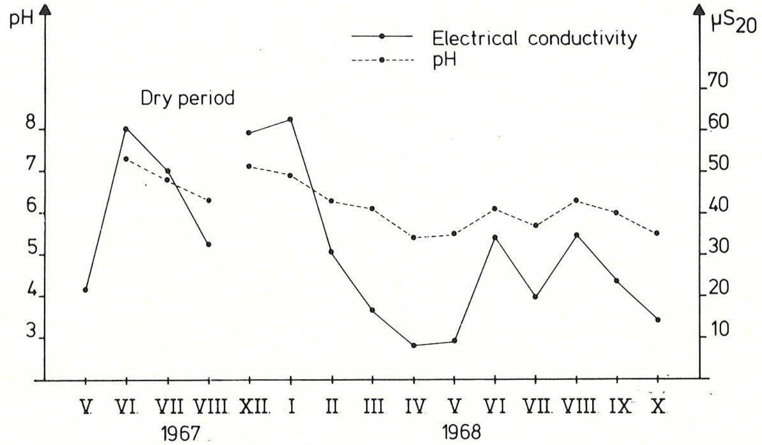

Fig.20: Lago Manacapurú: pH-value and electrical conductivity in the course of the year

Continual movement of the water maintained very favorable oxygen conditions through the entire stand of *Paspalum repens*. In open water, oxygen concentrations decreased gradually with increasing depth, but within the stands, there was a marked minimum at about 10 cm (fig. 21). In general, oxygen conditions were similar to those on Lago Calado, but movement of the water in this stand interfered with any strong development of the minimum, and oxygen concentrations rose higher beneath the plant cover.

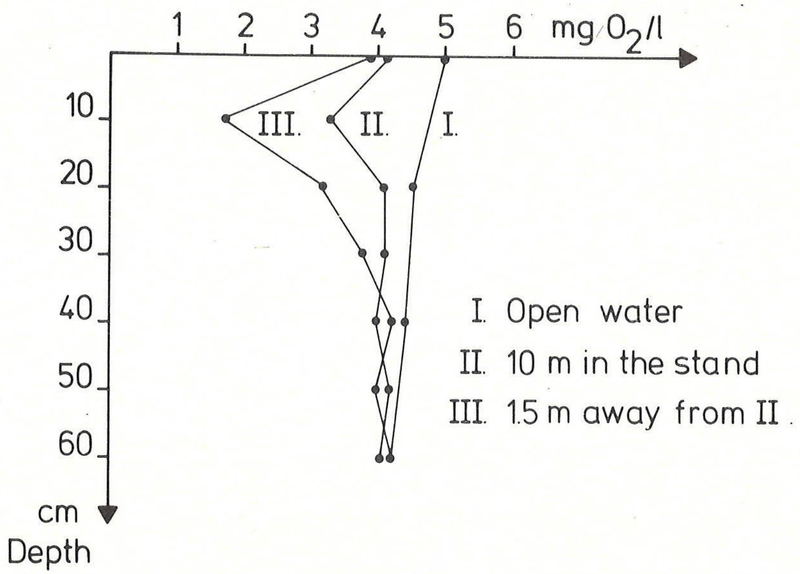

Fig. 21: The oxygen content in Paspalum repens - stand of Lago Manacapurú (11.8.1968)

The faunal community:

Total abundances in 1968 showed a small maximum just at the beginning of faunal development (fig. 22 a). Abundances were very low for the next five months. In June, they began to increase toward the primary maximum of 593 800 individuals per m^2 in September. Just before the biotope dried up, numbers decreased again. All Crustacea combined and the Diptera, which were the most important groups numerically, reached absolute maxima at the time of the maximum total abundance. Only Copepoda and Cladocera joined Diptera to produce the initial maximum. Conchostraca first began to appear sporadically in January. As at the other stations, Ephemeroptera and Trichoptera had patterns of development very different from the fauna as a whole. Abundances were roughly the same on the periphery and in the inner portion of the stands. Ostracoda increased considerably toward the center of the stand, but Ephemeroptera and Trichoptera were much less numerous in the inner portions. Copepoda generally showed a similar decrease from the periphery inwards (fig. 22 c - i).

The small, early maximum abundance at the beginning of faunal development in December does not appear in the curve for total biomass (fig. 22 b). Otherwise, the biomass curve runs parallel to the abundance curve. An exception occurred in the June, 1968 sample from the peripheral zone, for which the dry weight was unusually high for the numbers of animals found. This was because Mollusca constituted 85 % of the biomass. This sample cannot be considered representative of the state of the community at that time.

Fig. 22 a - i: The aquatic fauna in the floating vegetation of Lago Manacapurú in the course of the year.

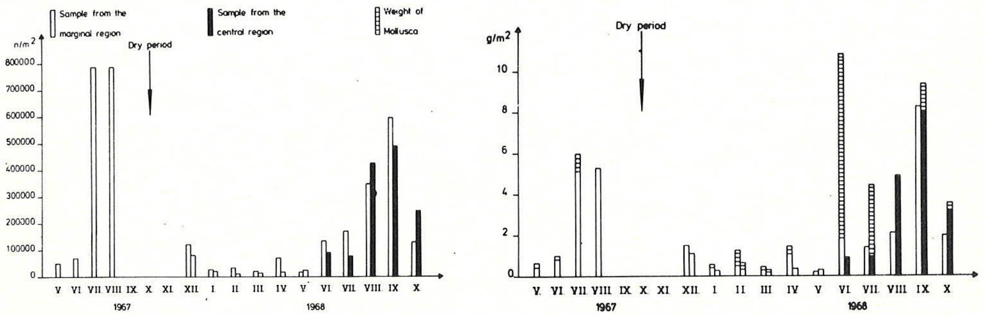

Fig.22a: Total number of individuals

Fig.22b: Total dry weight (without large individuals)

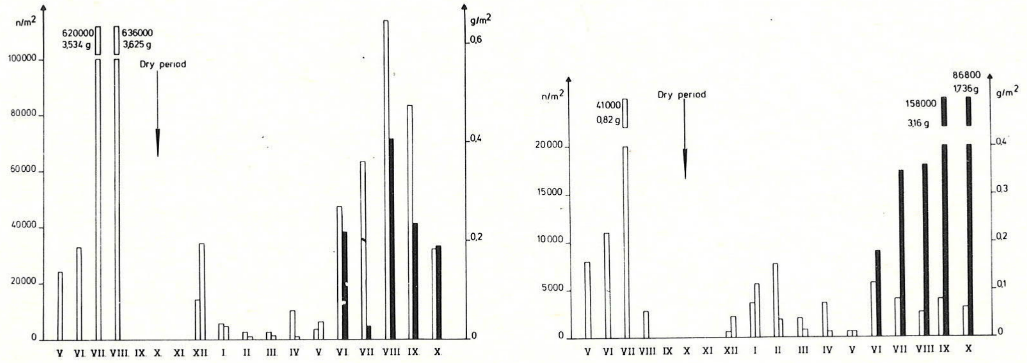

Fig.22c: Copepoda

Fig.22d: Ostracoda

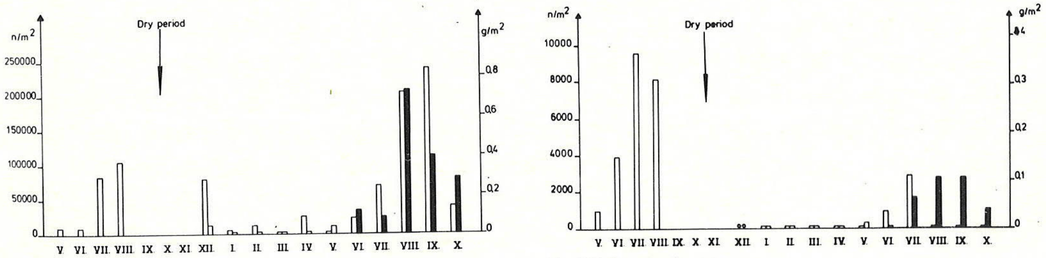

Fig.22e: Cladocera

Fig.22f: Conchostraca

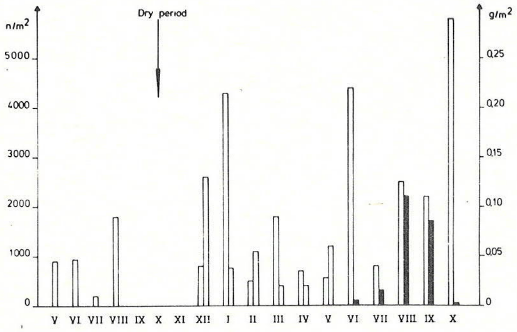

Fig. 22g: Ephemeroptera

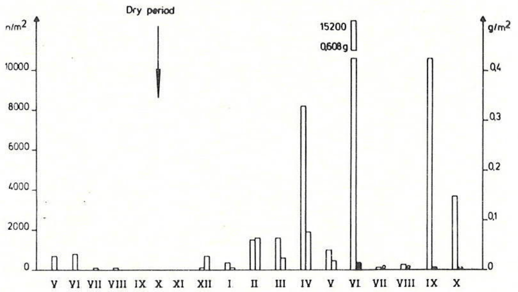

Fig. 22h: Trichoptera

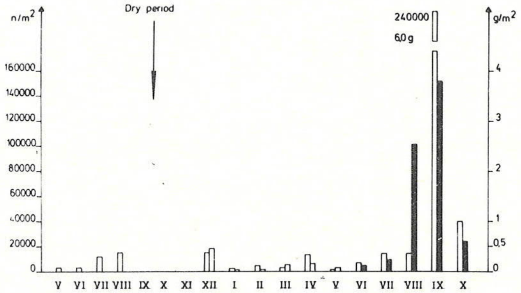

Fig. 22i: Diptera

Total biomass, including the average weight of larger animals (2.22 g)[1], fluctuated between 2.5 and 3.7 g dry weight per m^2, then increased to 11.6 g/m^2 in September. With separate calculation of the molluscan contribution, this is equivalent to a wet weight[2] of about 12 - 19 g/m^2 through May, and 62 g/m^2 during the September maximum. The biomass of Diptera rose as high as 6 g dry weight/m^2 (approximately 36 g wet weight)!

In contrast, the maximum of the preceding year (786 500 individuals per m^2) was composed mainly of Copepoda. The greatest abundance of that group was 636 000 per m^2. This abundance produced a dry weight of 3.63 g/m^2 (about 25 g wet weight)! As far as we can determine, these are the highest abundances ever reported from tropical inland water!

We offer the following explanation for the observed fluctuations in faunal abundance.

As the water level rose, terrestrial grasses which had taken hold on the beaches during the dry season were drowned. they gradually produced large floating masses of rotting organic matter in places protected from the wind and current, and mixed with the first growths of floating vegetation. One sample, which was taken in December 1967 from dead plant matter, shows the early development of the fauna among these flooded, and later, floating grasses. Soon however, the remains of these grasses were carried away by the current. Animals living among them drifted away or moved over onto the roots of the floating vegetation. Faunal abundance remained fairly stable during the following months. During these early months, however, the available habitat itself was increasing rapidly in extent in this biotope, as well as in all the others in the study. Thus constant density should not be interpreted as a cessation of faunal development.

It is clear, nevertheless, that a maximal density was achieved very quickly, and could not be exceeded at those levels of environmental factors. This density was low relative to other várzea lakes. A pattern parallel to that previously described for whitewater biotopes is recognizable. In these, too, a maximal density supported by the combined effects of current and amounts of suspended,inorganic solids was quickly attained and sustained. This combination of effects occurred only briefly in Lago Manacapurú. Even though a slight current was usually present, the *Paspalum repens* stand was thick enough to protect all but the most peripherally located animals from the danger of being carried away in the drift. There were no detectable suspended inorganic solids from March on.

A striking correlation existed between abundance and conductivity. In December conductivity was high, a current sufficient to carry away floating masses of dead grass had not yet developed and transparency was about 70 cm. It was then that the first small maximum occurred. In January, the area was completely under the influence of whitewater, accompanied by increased currents, lower transparency and relatively high conductivity. Except for brief interruptions, these conditions persisted at least until February. Just as in Lago Calado, the rate of influx of whitewater depends mostly on the rapidity with which the water level rises in the Solimões and the amount of runoff from the terra firme. The causes of occasional increased transparency and reduced currents which were observed in January were probably the same as those acting in the mouth region of Lago Calado. Thus, such fluctuations can occur repeatedly but irregularly.

During the period of whitewater influence, abundance was apparently limited by currents and amounts of suspended, inorganic solids. The potential effect of these factors is greater at that time when the stands are young and relatively sparse.

Whitewater influence ceased after March. Still, abundances did not increase. The conductivity curve shows that, at that time, a strong, steady input of electrolyte-poor, terra firme water was already under way. This input increased in the following period and finally suppressed all traces of whitewater influence. Only in July did conductivity, pH and other factors indicate a resurgence of that influence. A heavy bloom of Cyanophycea (*Microcystis*) was observed then near the sampling station in locations which were protected from the current. Also during that period, the numbers of individuals per m^2 increased considerably. Peak conductivities in August and June were evidence of the effects of whitewater, but the simultaneously high transparencies show that its load of suspended solids had been removed from the water by sedimentation. Most of this water probably came from Lago Cabaliana, which joins Lago Manacapurú near its outlet (fig. 2, see p. 22). During this period, a higher concentration of animals, both in number and biomass, was observed at this station than at any other time or place in this investigation.

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[1] See p. 19 f. for derivation of this value.

[2] See p. 19 f. for the method of calculating wet weights from dry weights.

The extremely large numbers which formed this maximum were probably the result of a very favorable combination of plentiful food, transparencies and weak currents. The slight current prevented stagnation, which could have led to depletion of the nutrients in the euphotic layer, and continually renewed the suspended materials and phytoplankton among the root masses. The bloom of blue-green algae in July shows that autochthonous phytoplankton production was possible under these conditions.

The first collections at this station during 1967 confirm this explanation for the changes in abundance. These samples also show a large increase in numbers of animals shortly after an increase in conductivity. The effects of the current have already been discussed for the case of Lago Calado.

Further evidence for the effects of low electrolytes and input of suspended materials on the fauna comes from the author's investigations in electrolyte-poor waters of the Rio Negro and a rivulet in the terra firme (JUNK 1969). The same type of wire boxes with excelsior that was set out in Lago Calado was used as an artificial substratum. In those studies, too, total abundances were relatively low in comparison to the várzea lakes, which are richer in electrolytes. Faunal densities were significantly greater, however, where sufficient quantities of detritus were washed into the excelsior by the current.

It is evident here, as in the earlier case of the Paraná do Xiborena, that brief changes in environmental conditions have little or no detectable influence on total biomass. Those animals which react most readily to such changes, particularly Cladocera and Copepoda, generally have little effect on total biomass because of their small size. On the other hand, such larger and often irregularly occurring forms as the Mollusca have an influence on total biomass quite out of proportion to their abundance or indicative significance, and can produce misleading patterns. An example of this can be seen in the June, 1968 sample from the peripheral zone. A chance aggregation of Mollusca produced an apparent, absolute maximum in dry weight which did not really exist. The proportion of Mollusca in total numbers, however, was far less influential, so that these values reflect the existing conditions much better.

The case of Lago Manacapurú shows that electrolyte concentrations can become limiting for the fauna below a certain level. This control is obviously mediated through the interaction between plant nutrients and phytoplankton production, which in turn determines the quantity of food available to the fauna. The effects of different species composition of the phytoplankton, and direct influence of low electrolyte concentrations and pH values on the abundance and species composition of the fauna are special problems requiring special investigations.

5. Lago do Xiborena

Description of the biotope:

Lago do Xiborena is a long, narrow várzea lake about 15 km from Manaus, which flows out into the Paraná do Xiborena. To judge from its shape, it must have been formed from an earlier bed of the Paraná do Xiborena after it changed course. As long as any water remains in the canal, the lake retains a narrow connection with it. In 1967, this connection lay dry during October and November. The lake dried up except for a small pool about 300 m x 30 m in area, with a maximum depth of only 1.5 m. Beneath this pool was a thick layer of partly blackish, rotten-smelling mud. The wind stirred materials into the water during this period such that transparencies were reduced to only 30 - 40 cm (fig. 23). Much of the floating vegetation dried up, but there were a few floating stands left in the pool at its lowest water level. These were mostly *Paspalum repens. Echinochloa polystachya* was barely represented, for this grass had been harvested by the people living around the lake as cattle forage during high water levels wherever the cattle had not already eaten it away.

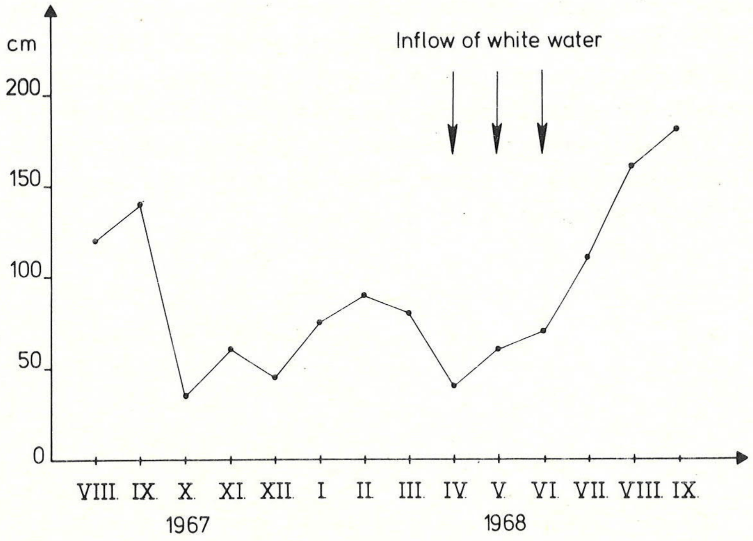

Fig. 23: Lago do Xiborena: Visibility in the course of the year

Pistia reproduced rapidly during the months from October to December. As soon as a connection with the Rio Negro was re-established via the Paraná do Xiborena, most of the sparse stands of this species were washed out. In February and March *Azolla* and *Salvinia* began a rapid development. Other floating plants characteristic of varzea also began reproducing at this time, but less vigorously, including *Eichhornia, Reussia, Neptunia, Limnobium, Ceratopteris,* etc. Near the outlet of the lake, *Victoria regia* appeared. In April, the water levels were rising so fast that whitewater flooded over the leveé of the canal through the forest and into the lake. Currents with speeds between 5 and 20 cm/sec flowed through the full length of the lake. At that time, the lake still had large stands of *Paspalum repens*, but these were mostly carried away as water continued to rise in May. By July the water had begun to fall and whitewater no longer carried its load of suspended solids into the upper section of the lake, as can be seen in the rapidly increasing transparencies.

Physical - chemical investigations:

From October until January, pH's remained near neutrality. From February through September, they varied between 6.3 and 6.6 under the increased influence of fresh whitewater (fig. 24). Conductivities underwent a pattern of change which was unusual for the Amazonian region. Normally, conductivities in this area increase to a maximum of about 80 μS_{20}. In Lago do Xiborena, however, values in excess of 300 μS_{20} were measured from October until December. In this small, enclosed, shallow body of water, it appears that large amounts of organic mud and continual stirring can produce high conductivities as a result of remineralization processes. A simple experiment, although it was actually intended to detect the presence of dormant stages of aquatic animals, confirmed this hypothesis. Dried organic material derived from the floating vegetation in Lago Calado was placed in a flask of water from the Solimões river. The flask was stoppered with cotton and aerated for four months. By the end of that time, the conductivity of the water in this vessel had risen to 326 μS_{20}. A control flask with pure Solimões water underwent a much smaller increase, to 83 μS_{20}. Both vessels lost about 20 % of the volume of water to evaporation.

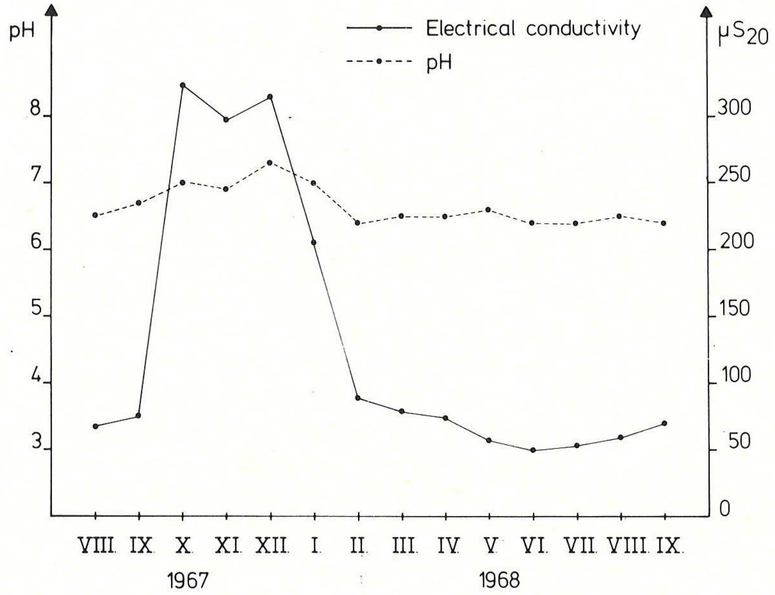

Fig. 24: Lago do Xiborena: pH-value and electrical conductivity in the course of the year

As soon as a connection between lake and canal was re-established, dilution and exchange of water lowered the conductivity to normal levels, and there was no further increase until the end of the year during low water levels. The influence of these processes in the Paraná do Xiborena has already been discussed. This case clearly shows that considerable amounts of gyttjas, or organic muds, can be found even in some of the polymictic várzea lakes of the Amazonian region. They are formed in spite of the greater speed of remineralization processes at higher ambient temperatures. When water levels are low, the regeneration of electrolytes from the mud has a pronounced effect on the conductivity of the water. An additional factor, which we shall call the 'sediment factor', operates similarly to the 'shore factor' in várzea lakes to increase electrolyte concentration[1]. The conditions which must exist for these factors to be effective are different, however. The 'shore factor', to follow BRAUN's (1952) definition, depends on rising water levels. It operates as the area of a body of water is enlarged. The electrolytes which enrich the water come from newly flooded shore areas, i.e., from soils which were not previously covered with water (McLACHLAN 1971). The 'shore factor' acts in opposition to a 'dilution factor', which is relatively less effective initially. In contrast, the 'sediment factor' first operates when water levels have fallen. Thus it is not opposed by the 'dilution factor'. Rather, the volume of water covering the decomposing mud decreases and the effect of this factor becomes stronger. At the same time, the area of the body of water is decreasing. Enrichment of the water with electrolytes is effected from the floor of the lake, not its shores.

Of course, the effectiveness of the 'sediment factor' ultimately depends on the amount of remineralizable substances available in the bottom of the lake. In Lago do Xiborena, these substances are derived largely from floating vegetation which can cover as much as 75 % of the surface of the lake for short periods. None of the other investigated lakes showed conductivity increases of nearly the magnitude which was observed in Lago do Xiborena.

Oxygen concentrations in the inner portions of *Paspalum repens* stands were not studied in this lake, since the consistent results from Lago Calado, Lago Manacapurú and Lago Parú allowed us to assume that values were similar in Lago do Xiborena.

The faunal community:

Samples of aquatic animals were taken from stations at the upper end of the lake and near its outlet.

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[1] Extensive investigations of the regeneration of nutrients from lake sediments have already been conducted by several authors in European lakes (OHLE 1938, 1964, UNGEMACH 1960, MORTIMER 1941/1942, ROSSOLIMO, L. 1939, etc.).

Station 1 (upper end of the lake)

Total abundances underwent wide fluctuations in the course of a year (fig. 25 a). From October to January, abundances were very high. After that, they decreased sharply, reached a minimum between May and July, and then increased again beginning in August. With minor exceptions, this pattern was the same for the separate groups: Cladocera, Ostracoda and Diptera. Conchostraca, Ephemeroptera and Trichoptera had different patterns (fig. 25 c - i). Conchostraca were very rare during the period of minimum total abundances from May to July, however.

This pattern of abundances was less clearly apparent in the biomass data (fig. 25 b). The October-January maximum was less pronounced. An unexpectedly high dry weight (relative to the number of individuals) occurred in one sample in April. In this case, as for similar deviations at other stations, the cause was the high proportion of Mollusca (67 % of the total weight). If this group is excluded from the biomass, a pattern similar to that for total abundance shows up. The absolute total biomass may be determined by adding the mean weight of the larger, presorted animals to the dry weights shown in the graph. This mean weight was 2.22 g1).

Including that amount, the total biomass at the upper end of Lago do Xiborena during the period of study fluctuated between 2.8 g and 6.3 g dry weights per m^2. Calculation of wet weights, with a separate conversion factor for Mollusca, yields estimates of 13 - 28 g/m^2.

We must say more about the importance of transparencies for the aquatic fauna before we can proceed with our explanation for the observed changes in abundance.

Transparencies were high in September, decreased to the lowest value measured during the entire period in October, remained very low in December, then reached a small submaximum in the following months. A second minimum occurred in April, followed by an increase from July through September (fig. 23). The coincidence of the absolute minimum transparency (30 cm) in October with the extremely high total abundance (300 000 individuals/m^2) at first seemed to be in strong contrast with results of our other investigations. At all the other stations, such low transparencies had a negative effect on the fauna.

What we see here cannot be explained by considering transparency to be an independent factor, separated from other factors which act with it. Rather, an explanation is to be sought in the effects on the aquatic fauna of those factors which were responsible for the low transparencies.

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1) See p. 19 f. for calculation of this value.

Fig. 25 a - i: The aquatic fauna in the floating vegetation of Lago do Xiborena (upper end of the lake) in the course of the year.

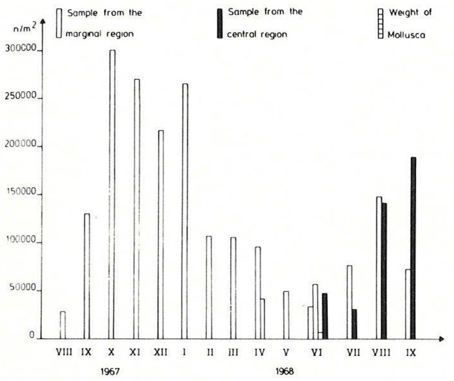

Fig.25a: Total number of individuals

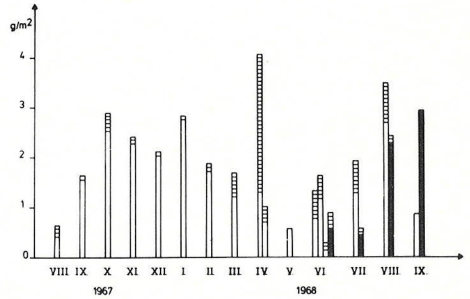

Fig.25b: Total dry weight (without large individuals)

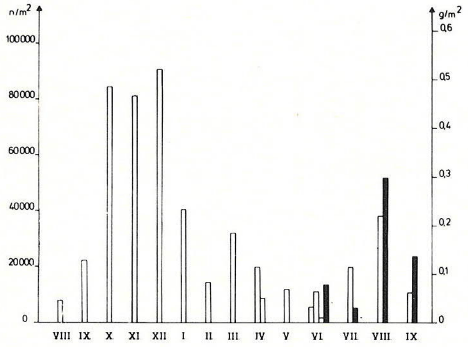

Fig.25c: Copepoda

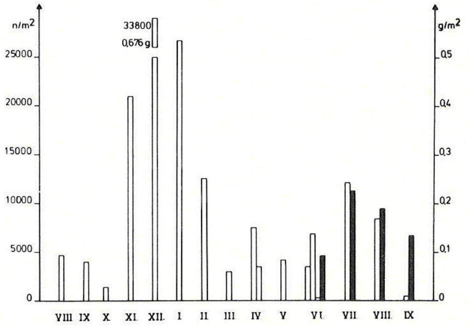

Fig.25d: Ostracoda

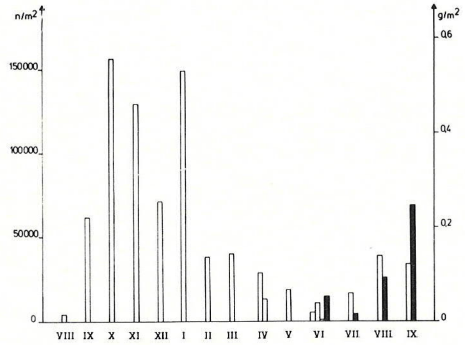

Fig.25e: Cladocera

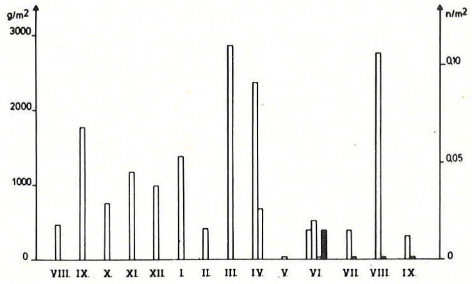

Fig.25f: Conchostraca

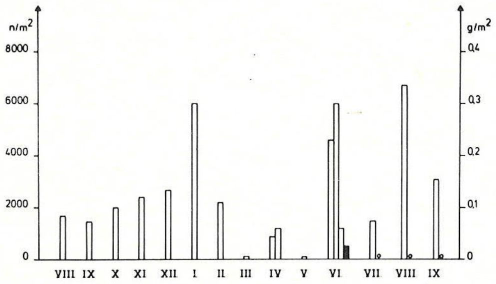

Fig.25g: Ephemeroptera

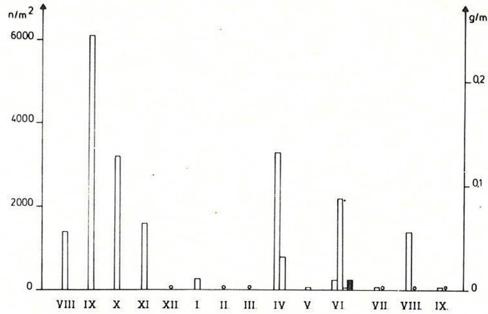

Fig.25h: Trichoptera

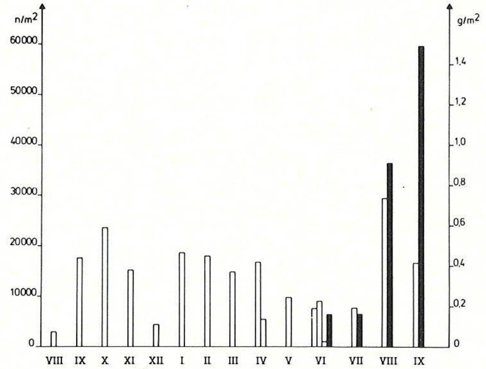

Fig.25i: Diptera

In September, 1967 Lago do Xiborena was still relatively deep. The transparency was 130 cm and conductivity had increased to 100 μS_{20}. Studies in Lago Manacapurú led to the conclusion that conductivity was highly correlated with the available nutrients for phytoplankton. Therefore, the conductivity was relatively favorable for phytoplankton production.

In October, conductivities rose above 300 μS_{20}, and by implication there must have been nutrients present to favor the growth of phytoplankton. Despite occasional stratification of the water, which could lead to a decrease of up to 1°C through the upper water layers in calm weather and strong sunlight, transparency was very low. This was because of wind action, feeding activities of fish, etc. in the now very shallow lake, which hindered the sedimentation of finer particles from the disturbed bottom. Nevertheless, membrane filtration of the water revealed large quantities of phytoplankton in spite of the low transparency1). This may be attributed to the shallowness (maximum depth

1) SCHMIDT (1973) found under these conditions the highest phytoplankton concentrations in the várzea lakes.

ca 1.5 m) and absence of currents. Thus the food supply for the fauna was sufficient to enable development of the observed maximum abundance. This shows that a fundamental distinction exists between the flowing whitewater of the Solimões and the turbid, stagnant water of shallow lakes. This distinction has been mentioned above in the case of the Paraná do Xiborena. In the former type of water, the suspended material is almost exclusively inorganic (GESSNER 1959), but the water in stagnant lakes allows phytoplankton production and contains organic material in suspension which was stirred up from the bottom. The effects of the two types of turbidity on the aquatic fauna, as we have shown, are fundamentally different.

From October until December, the low transparencies in Lago do Xiborena were due to low water levels.

Beginning in January, the water levels were high enough so that the various sources of turbulence were no longer adequate to stir up the bottom. Transparencies increased as suspended material slowly sedimented. By February, the water in the lake had been diluted or exchanged as can be seen from conductivity values and the animals declined to only a third of their original density. Even so, the residual abundance of 100 000 per m^2 was still near the average for other várzea lakes, such as Lago Calado.

In April, the water level had risen so high that whitewater from the Paraná do Xiborena, with its heavy load of suspended solids, penetrated through the surrounding forest, over the leveé and into the lake. It flowed through the lake at speeds of 5 - 20 cm/sec. The resulting, second minimum in transparency was therefore of different origin from the first, and had a very different effect on the fauna. Total abundance decreased to a minimum. In July, the water levels had already begun to fall, and there was no current. Transparencies increased again to a maximum in September; the animals increased correspondingly. In September, the connection between the lake and the Paraná do Xiborena had become very narrow, and conductivities slowly began to rise again. Although this discussion has produced some reasonable inferences about cause and effect among these processes, final clarification would require a combination of long-term analyses of the water with parallel, quantitative studies of primary production.1)

Again in the Lago do Xiborena, it was clear that changes in environmental factors are especially evident in their effects on the abundance of animals which have shorter lifespans (i.e., mostly Crustacea).

Station 2 (lake outlet)

The patterns shown by the histograms for total abundance and abundances of the separate groups over the year were approximately the same as at station 1 (fig. 27 a - i). The

1) Such investigations have been conducted from 1967 to 1969 in the vicinity of Manaus by Dr. G. W. SCHMIDT and have confirmed our data (personal communication).

annual cycle of transparencies shows that the small submaximum which occurred at the upper end of the lake was not developed here (fig. 26). This was due to the slow invasion of whitewater from the Paraná do Xiborena. The speed of the corresponding current was so slow, however, that no water movement could be detected between Paraná and lake, and the water was practically still at the sampling station. In good weather, the upper 40 cm were thermally stratified. These conditions allow us to assume with confidence that sufficient phytoplankton production was taking place. Therefore, values found at station 2 can be considered as a confirmation of the results obtained at station 1.

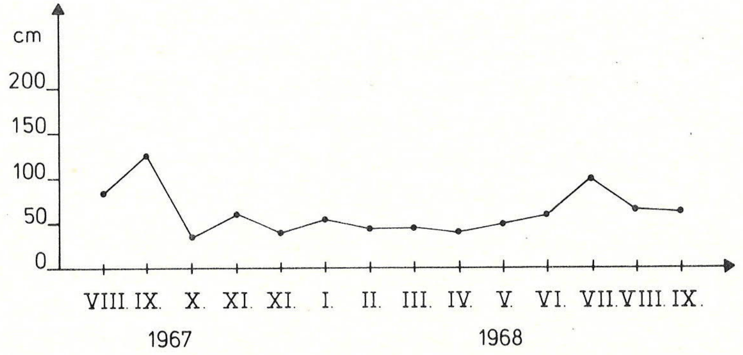

Fig. 26: Lago do Xiborena (lake outlet): Visibility in the course of the year

Fig. 27 a - i: The aquatic fauna in the floating vegetation of Lago do Xiborena (lake outlet) in the course of the year.

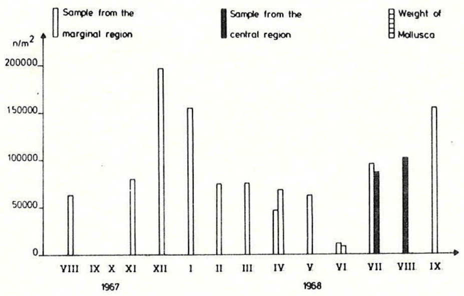

Fig.27a: Total number of individuals

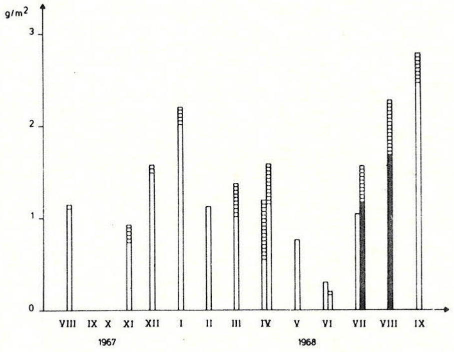

Fig.27b: Total dry weight (without large individuals)

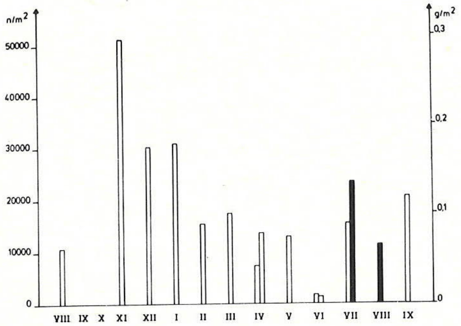

Fig.27c: Copepoda

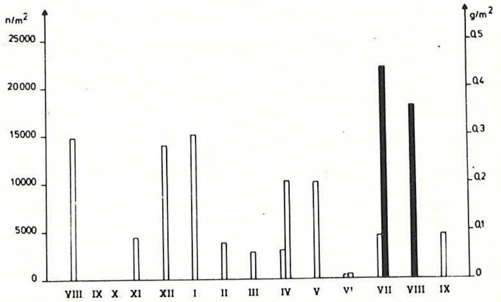

Fig.27d: Ostracoda

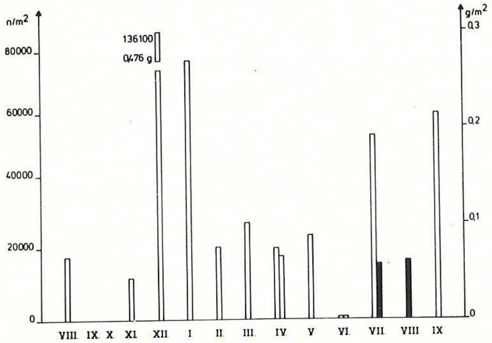

Fig.27e: Cladocera

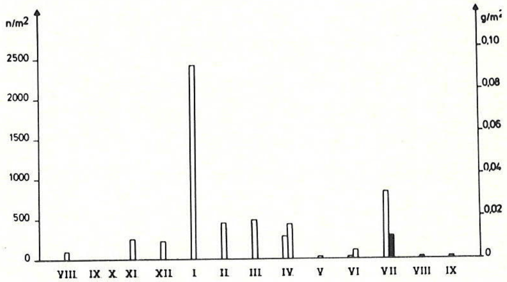

Fig.27f: Conchostraca

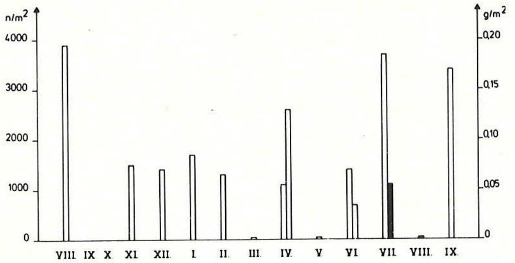

Fig.27g: Ephemeroptera

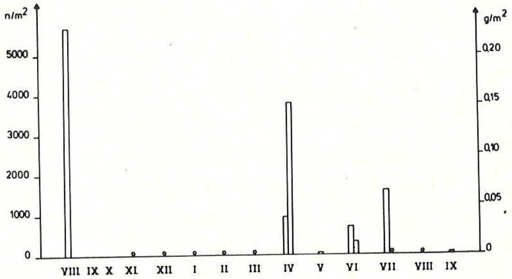

Fig.27h: Trichoptera

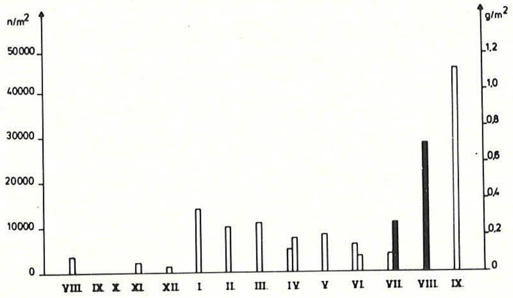

Fig.27i: Diptera

6. Lago dos Passarinhos

Description of the biotope:

Lago dos Passarinhos is a small, oval lake on the island of Careiro, about 25 km from Manaus. It is separated from the Paraná do Careiro by a leveé several hundred meters wide, and receives fresh whitewater from it for only a short time during extremely high water levels (fig. 2, p. 22). Precipitation is sufficient to keep the lake from drying up, even during the dry season. Although the water level in the lake fluctuates several meters, the depth of the lake is great enough to prevent wind action from stirring up the bottom and producing high turbidities as it does in Lago Calado and Lago do Xiborena. A continuous belt of floating vegetation extends all the way around the lake throughout the year, leaving free only a narrow strip along the shore. This narrow strip is adjacent to pastureland, and presumably is produced by cattle, which graze on the floating vegetation. Three zones can be distinguished clearly in this belt of floating plants. Near shore, *Leersia hexandra* is dominant, partly as a terrestrial or palustrial form, and partly floating. Lakeward of this zone is an almost continuous band of *Scirpus cubensis*, and then a narrow strip of *Paspalum repens*. The stands are intermixed only on the periphery and 'secondary colonizer' species are rare or absent. *Echinochloa polystachya, Paspalum fasciculatum, Oryza, Panicum chloroticum* and *Hymenachne amplexicaulis* do not occur. This lake belongs to the type of biotope described in Part I, Chapter V, which deals with várzea lakes having relatively small fluctuations in water level (JUNK 1970).

The investigations we have discussed so far were concerned with the fauna of floating stands which last only one year. At the end of the year, they decompose rapidly, so the thickness of the stand is limited to a year's growth. This is not true for *Leersia hexandra* and some species of the family Cyperaceae as has already been mentioned in the species descriptions in Part I. The dead plants decompose more slowly, and under certain circumstances, can build thick polsters in combination with living sprouts over several years. Samples were taken to determine the effect of this greater thickness on oxygen concentrations in the inner parts of the stands, and how it affects the aquatic animals.

Physical - chemical investigations:

Transparencies in the lake were about 80 - 90 cm. The color of the water was greenish. Conductivities varied between 30 and 40 μS_{20}, and pH values were slightly acid (5.9 - 6.6).

Oxygen determinations in the inner part of the *Leersia hexandra* stand yielded a similar pattern to that found in dense stands of *Paspalum repens*: high oxygen concentrations at the surface, rapid decrease downwards into the roots, and a slight increase at the lower margin caused by an influx of oxygenated water from open areas (fig. 28 a - c). Sometimes, however, oxygen was completely absent from these stands and H_2S was formed, a phenomenon never observed in biotopes described earlier (fig. 28 b). The formation of the latter gas resulted from the much denser structure of the multiannual stands. Also, this grass often formed large, low hummocks which rose above the water and interfered with oxygen replenishment from the air in the upper few centimeters of water (see also Lago Parú and Lago Castanho).

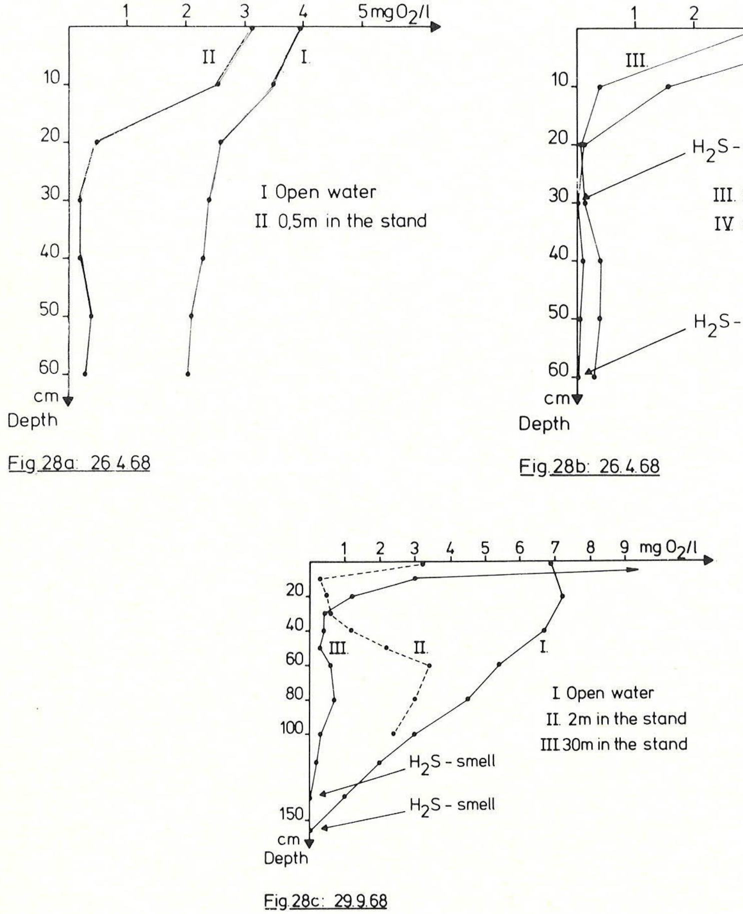

Fig.28a: 26.4.68

Fig.28b: 26.4.68

Fig.28c: 29.9.68

Fig 28a-c: The oxygen content in Leersia hexandra-stand of Lago dos Passarinhos

The volume of water in the lake was sufficiently great to obscure the effect of the 'sediment factor', so in spite of its isolation, the lake never received an increase in conductivity from this source. In fact, the conductivities of 30 - 40 μS_{20} were much lower than in the Amazon, so it must be assumed that a significant dilution with electrolyte-poor rainwater had occurred. As the following results will show, however, neither dilution nor preceding isolation from the Amazon for one or more years had a negative effect on the fauna. This implies that conductivity does not become a limiting factor for faunal abundance in the 'floating meadows' of the várzea, either directly or indirectly, until it falls below 30 μS_{20} (see also Lago Manacapurú).

The faunal community:

One sample, taken in November 1967 from the narrow band of *Paspalum repens* shows that the fauna in this lake was similar to those in the other várzea lakes we investigated. All the same faunal groups were represented. Conchostraca, which had proven to be a characteristic faunal element in várzea lakes, were very abundant (Table 9). Faunal abundances at that time were still higher along the margins of the *Leersia hexandra* stands where this species bordered open water (Table 9). This sample was marked by an unusually high abundance of Ostracoda: 203 500 individuals/m^{2} in comparison to 46 800/m^{2} in the band of *Paspalum repens*. On the other hand, Cladocera were much more numerous among the *Paspalum repens* (116 800/m^{2}) than in the *Leersia hexandra* (32 700/m^{2}). These differences can be attributed to the greater density of the *Leersia hexandra* stand at its edge. This favored the poorer swimmers, while the more open stands of *Paspalum repens* favored good swimmers. The greater abundance of the predominantly sessile Conchostraca on the edge of the *Leersia hexandra* stand can also be construed as supporting this explanation, although the difference between densities at the two locations (6300/m^{2} vs. 3300/m^{2}) cannot be given great emphasis because of the local heterogeneity in abundance.

In general, abundances were high in this lake. The entire peripheral region at the time of sampling had abundances between 160 000 and 360 000 individuals per m^{2}. Dry weights, including the mean weight of larger animals over all samples of 2.22 g, was between 4.9 and 10.2 g/m^{2}. With a separate conversion factor for molluscs, this is equivalent to a wet weight of about 25 - 54 g/m^{2}. These values for abundance and biomass in the peripheral zone of the vegetation in Lago dos Passarinhos are about twice as large as those from Lago Calado.

Only a few meters into the inner part of the *Leersia hexandra* stand, however, there were fundamental differences from the previously investigated *Paspalum repens* stands. Total abundance dropped off abruptly (fig. 29 a). Ephemeroptera, Trichoptera and Conchostraca were totally absent, and all other groups were very sparsely represented (fig. 29 c - i). The Ostracoda seemed to be the best adapted to the conditions existing in the inner part of the stand. Although their absolute abundance decreased, the proportion of total fauna which were Ostracoda increased considerably (Table 10). No larger animals occurred there even near the surface where dissolved oxygen was available, because of the denseness of the plant mass. Therefore, the biomass shown in the figure in this case is the same as total biomass. In the central zone, dry weights were 0.16 and 0.20 g/m^{2} (fig. 29 b). The equivalent wet weights were 1.0 to 1.8 g/m^{2}.

One sample seems to present a contradiction to these results (fig. 29 a - i). It was taken about 30 m into the stand in September 1968. This sample not only contained a large

Table 9: Parallel samples from neighboring stands of *Paspalum repens* and *Leersia hexandra*.

Date	24.XI.67	24.XI.67
Species of Plant	*Paspalum repens*	*Leersia hexandra*
Faunal Abundance		
Copepoda	37 300	49 000
Ostracoda	46 800	203 500
Cladocera	116 800	32 700
Conchostraca	3 300	6 300
Decapoda	+	–
Hemiptera	270	+
Odonata	320	+
Coleoptera	+	2 500
Ephemeroptera	3 900	13 800
Trichoptera	540	1 000
Diptera	21 900	26 400
Hydracarina	17 300	16 300
Mollusca	5 200	3 800
Oligochaeta	8 700	3 800
Total Abundance	262 330	359 100

Table 10: Percentage of total abundance due to Ostracoda in the floating vegetation of Lago dos Passarinhos.

		Zone	
Date	Peripheral %	Transitional %	Central %
24. 11. 67	17.7	–	66.4
	56.3		
26. 4. 68	25.7	30.1	71.6
29. 9. 68	9.0	–	56.0

number of individuals, but Conchostraca were present. Oxygen concentrations were measured very near the site of this sample, however. These measurements revealed several aspects of the biotopic conditions and provide a clear explanation for this inconsistency (fig. 28 c). Judging from the curve, there was a plentiful supply of dissolved oxygen in the upper 20 cm of water. This was caused by a local feature of the stand. One area of the

Fig. 29 a - i: The aquatic fauna in the floating vegetation of Lago do Passarinhos.

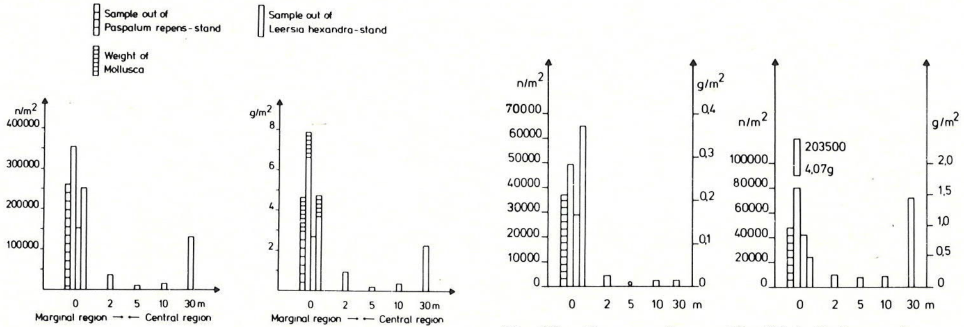

Fig.29a: Total number of individuals

Fig.29b: Total dry weight (without large individuals)

Fig.29c: Copepoda

Fig.29d: Ostracoda

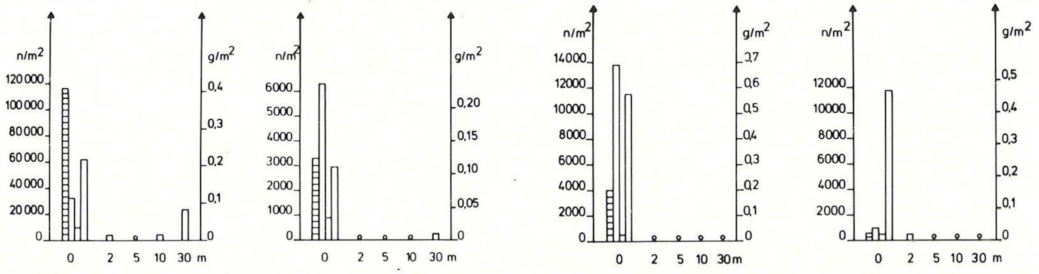

Fig.29e: Cladocera

Fig.29f: Conchostraca

Fig.29g: Ephemeroptera

Fig.29h: Trichoptera

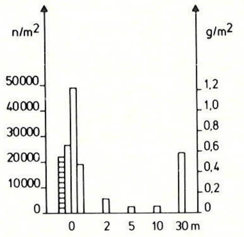

Fig.29i: Diptera

stand had sunken some 20 or 30 cm below the surface of the water and was supported in this position by surrounding plants. Unlike the rest of the stand, which was covered by only a few centimeters of water at the most, this section was covered by several square meters of relatively open water up to 20 cm deep, penetrated only by fresh shoots. Conductivity in this water was only 25.3 μS_{20}, and the pH was 6.0. At the same time, the corresponding values for open water outside the stands were 42.7 μS_{20} and 6.6. These indicate that such small areas of water are essentially isolated from open water by the dense mass of plants, and are more strongly influenced by rainwater. This special biotope offered favorable living conditions for aquatic animals. In addition, a bloom of Cyanophyceae occurred, producing a supersaturation of oxygen. Although this case is not characteristic for stands of *Leersia hexandra* in general, it does show how intensively the aquatic plants and animals utilize any space which provides even a marginally adequate habitat. This case further supports the viewpoint expressed in the preceding section, that fine differences in the structure of the vegetation which are very difficult to evaluate quantitatively can have great influence on the character and density of the biotic community.

The abrupt decrease in faunal abundance and depletion of oxygen from the water underlying the compact mass of plants indicates that such dense stands are at least temporarily unsuitable as habitats for fish. In fact, the O_2-minimum for many fish species can be reached and passed by depletion processes under large stands, especially in sheltered inlets during calm weather (GEISSLER 1969). Native fishermen also report that few fish are caught in the *Leersia hexandra* zone around Lago dos Passarinhos.

7. Other Stations

Additional samples were taken at several other stations to support the observations reported above. They will be dealt with briefly in the following section.

Lago Parú

Lago Parú lies near Lago Calado (fig. 2). It is connected to the Solimões all year. When the samples were taken, the pH was 5.9, conductivity 28.6 μS_{20}, transparency 230 cm and the water color was olive.

A well-developed stand of *Paspalum repens* and *Echinochloa polystachya* was chosen as the sampling site. At the time of sampling (11.8.1968), the stand was showing signs of senescence. Near it was a very old floating island over 1 m thick. The original vegetation (*Leersia hexandra* and various species of the family Cyperaceae) was evident only around the edges. The entire inner region of the island was populated by 'second colonizers'. A more detailed description of this island has been given in Part I.

Comparison of oxygen concentrations clearly shows the difference between the two biotopes (fig. 30, Table 11). The *Paspalum repens* stand exhibited a typical oxygen distribution as described above, but the water in the floating island was nearly oxygen-free from the edge inward. The aquatic fauna reflected these conditions. The *Paspalum repens* stand had a total abundance of about 300 000/m^2 on the periphery, and about 200 000/m^2 in the interior. Dry weight, including the calculated mean for larger animals of 2.22 g, was 8.1 g/m^2 at the edge and 6.0 g/m^2 in the center. With separate calculation of the fraction due to Mollusca, these were equivalent to wet weights of about 42 g/m^2 at the edge and 32 g/m^2 in the center. Conchostraca were abundant in all parts of the stand. Trichoptera and Ephemeroptera were principally restricted to the peripheral zone, while Ostracoda were more abundant in the inner parts. Total abundance decreased by one-third from the periphery toward the center. In general, the faunal community was the same as those in the other várzea lakes which were investigated.

Table 11 : Oxygen concentrations in a dense, floating island in Lago Parú, (11. VIII. 68).

Depth (cm)	O_2 (mg/l) 1 m inward from the edge	O_2 (mg/l) 3 m inward from the edge
0	no water[1]	no water
10	0, odor of H_2S	no water
20	0.27	0.25
30	0.15	0, odor of H_2S
40	0, odor of H_2S	0.18
50	0, odor of H_2S	0.08
60	0.14	0.15
70	0.28	–

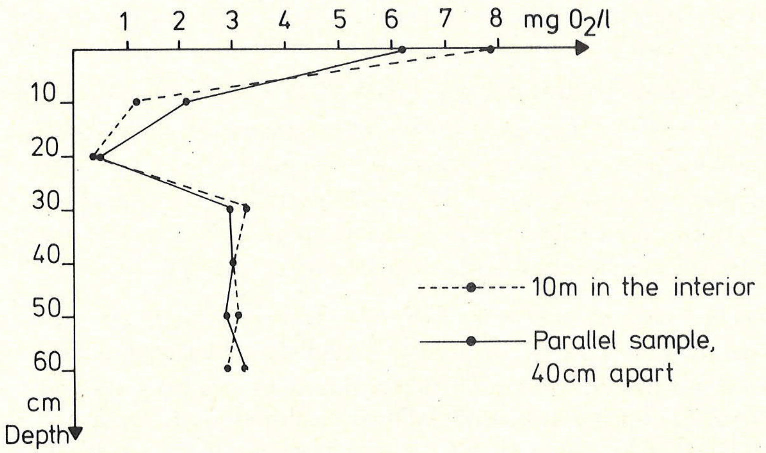

Fig.30: Oxygen content in a Paspalum repens population in Lago Parú (11.8.1968)

[1] The island rose more than 10 cm above the surface of the water in some places. "0" was the surface of the island.

No samples could be taken from the island by conventional methods because of its great thickness and dense consistency. Samples therefore consisted of plugs 10 x 10 cm in surface area and some 80 cm deep which were cut from the island where oxygen concentrations were measured. The material of the plug, which had a consistency like loose peat, was examined for animals. Not a single representative of any of the faunal groups we investigated could be found. From this, we conclude that the interior of the island was populated very sparsely, if at all, by these animals (see also the results from Lago Castanho).

Lago Castanho

Lago Castanho is situated on the right bank of the Solimões below the town of Manaquirí (fig. 2).

There was a large stand of *Leersia hexandra* and several species of Cyperaceae, which also included 'secondary colonizer' forms, in an inlet of this lake. The stand was very dense and about 40 - 50 cm thick. The outer edge was bordered by a band of *Paspalum repens* about 20 m in width, which showed definite signs of senescence on the sampling date (13.9.1968). The submerged roots on the edge of this band had been eaten away almost completely by fishes, so no representative sample could be taken from the peripheral zone. A sample from the inner part of this *Paspalum repens* band gave the following results: total abundance 180 000/m^2, Conchostraca present. Ephemeroptera were absent and Trichoptera rare. Including the 2.22 g from the calculated mean of all larger animals in the present study, the average dry weight was 6.2 g/m^2. This is equivalent to a wet weight of about 30g/m^2, when a separate conversion factor is used for molluscs. The fauna was about the same, therefore, as that occurring in *Paspalum repens* stands in várzea lakes, which have already been described.

In contrast, the adjacent, dense stand of *Leersia hexandra*, several species of Cyperaceae and 'secondary colonizers' was practically devoid of animals. (The sampling method was the same as that employed for the island in Lago Parú). By reaching through the sampling hole to the lower side of the stand, one could feel a thick layer of gas bubbles which were trapped by the mass of vegetation. These presumably constituted a formidable barrier to the animals, which might otherwise have dispersed into the root mass from the open water beneath it. In the central zone of the stand, H_2S was detected (fig. 31). Wherever water collected in depressions of the floating plant mat however, we observed Cyanophyceae, chironomids and other forms (see also Lago dos Passarinhos).

Lotic region of the Amazon

As we have pointed out in Part I, the free-flowing parts of the Amazon are not true, complete habitats for floating vegetation. The plants which occur there all originated under other conditions, either along the banks or in várzea lakes. Their original faunal communities must therefore have reflected the habitat in which they developed. When the vegetation in which they live passes out into the mainstream, such environmental factors as current speed and the quantity of suspended inorganic solids begin to exert a dominant influence. As we have seen, these factors have a strong effect on aquatic animals.

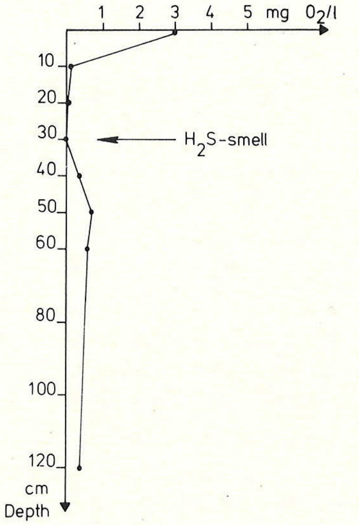

Fig. 31: Oxygen content in a dense floating island in Lago Castanho (25.9.1968)

During this study, several samples were taken from the peripheral zones of floating islands of *Paspalum repens*, interspersed with *Echinochloa polystachya, Pistia, Eichhornia* etc. As expected, the numbers of animals in the samples were similar to those in samples from the Paraná do Xiborena and the peripheral zones of stands on the Costa do Baixio, habitats also exposed to rapidly flowing whitewater. Total abundance were relatively low, between 7000 and 39 000 individuals per m^2. Except for a single sample, Conchostraca were absent. The mean weight of larger animals was calculated separately for this biotope. Including that amount (0.208 g), the dry weight varied between 0.32 and 0.92 g/m^2. Using the separate conversion factor for molluscs, we arrive at an equivalent wet weight of about 1.6 - 4.6 g/m^2.

Samples could not be taken from the central zones of these islands, for continual buffeting by the current had compacted them into a very dense mat there. Also, large chunks of driftwood usually had collected in them. Results from similar habitats indicate that only slightly greater abundances were to be expected in the central zones.

It remains to be determined how quickly the fauna changes after its substratum passes out into the mainstream of the Amazon. We may presume from the strong turbulence alone that changes are effected in the original character of the fauna within a short time.

Tapajós

The Tapajós is a typical clearwater river. At the time of sampling, its pH was 6.5 and the conductivity was 11.9 μS_{20}. The water was clear, with a transparency of more than 2 m and a greenish tint.

The lower reaches of the Tapajós are not at all favorable as a biotope for floating vegetation. Wave action, which can drive floating stands onto the banks, occurs daily on account of the river's great width. In some places, the shore is covered with a thick layer of dried *Paspalum repens* remains. Prof. SIOLI (personal communication) reports that aquatic and semi-aquatic vegetations find a true habitat in the river only in the parts 100 km and more above its mouth. This vegetation boundary corresponds to the lowest extent of the 'sedimentation zone' of the river.

Five samples were taken in June, 1968 from floating vegetation in the mouth area of the Tajapós. On the right bank about 15 km above Santarém, we came upon an island of *Paspalum repens* about 20 x 10 m in size, caught in the crowns of submerged bushes. The grass was infested with *Diatrea saccharalis* (Family Pyralidae), which had done it great damage. More than two-thirds of the uppermost shoots had been destroyed. The island had undoubtedly drifted down from another zone of the river.

One more stand of floating vegetation was discovered in a small blackwater several kilometers upstream from this site. According to residents of that area, the embayment formed an isolated pond during the dry season. Several small, sparse stands consisting of a species near *Echinochloa polystachya, Pontederia* spec. and a species of Cyperaceae were present. These stands probably developed in the blackwater, rather than having been washed into it by the river. One sample was taken from each stand.

The faunal community:

Total abundance was around 100 000/m^2. Conchostraca were present at all sampling sites. One sample was taken from the central zone of a *Paspalum repens* stand. Total abundance was slightly less in the interior than on the periphery of the stand. Ephemeroptera and Trichoptera were more numerous on the periphery, while Ostracoda preferred the central part of the stand. The rest of the stands were too small to allow differentiation between periphery and center.

The results can be interpreted only with great caution, for the number of samples is too small, and they represent at best only the situation in April. The stands were quite small. Transparency at the sampling site was more than 2 m, and there was no detectable current. The root bundles were clogged with detritus. In spite of the low conductivity, large quantities of algae were found in shallower water near the banks, which is evidence of a certain amount of primary production. Thus the biotopic factors which have proven to exert especially important effects on the fauna in the studies described above, i.e., transparency, current, oxygen concentration and available food, are of a similar nature to those in várzea lakes.

With this background, it seems justifiable to assume that the mean weight of larger animals for samples from várzea lakes (2.22 g/m^2) can be employed here, too. In fact, the samples included a large specimen of the genus *Ampullarius* (Family Pilidae) and about 100 small specimens of *Macrobrachium* (Family Palaemonidae). Under this assumption, dry weight fluctuated between 3.5 and 4.5 g/m^2. The corresponding range of wet weights is about 18 - 23 g/m^2. The samples provide only an initial insight into this lake, however.

Further investigations in the true habitat of floating vegetation in Tapajós will be necessary to determine whether relationships found in várzea lakes around Manaus are valid for the Tapajós.

IV. Discussion

1. Subdivision of the 'floating meadows' into three characteristic biotopes for the aquatic fauna

As one reviews the results from all stations visited during the investigation, the 'floating meadows' appear to fall into three major, fundamentally different biotopes on the basis of their aquatic faunas.

1.) The biotope of flowing whitewaters which are rich in suspended solids ('Whitewater Type').
This includes all stands in flowing whitewater rich in suspended solids: Paraná do Xiborena, lotic region of the Costa do Baixio, lotic zone of the Solimões-Amazon.

2.) The biotope in 'sedimented' whitewater, type A (Lago Type A).

This consists of relatively open stands with plentiful dissolved oxygen in the central region; such stands are usually found in lakes with mainly 'sedimented' whitewater: Lago Calado, Lago Manacapurú, Lago do Xiborena, shore region of the Costa do Baixio, Lago dos Passarinhos, Lago Parú, Lago Castanho, and possibly also the Tapajós, a clearwater river.

3.) The biotope in 'sedimented' whitewater, type B (Lago Type B).

This consists of thick stands with little or no oxygen and sometimes even containing hydrogen sulfide in the central region. These occur in lakes with mainly 'sedimented' whitewater: Lago dos Passarinhos, Lago Parú, Lago Castanho.

The distinctiveness of each of these biotopes is expressed in certain factors which both give it its typical characteristics and circumscribe its distribution. In the following sections, the ecological bases of the three biotopes will be elaborated from the results of the investigations presented above.

a) The 'Whitewater Type'

Two factors, current and concentration of suspended solids, characterize the Whitewater Type. Currents mix the surrounding water continuously and impede stratification. Any variations which arise are rapidly suppressed: for example, influx of small amounts of water poorer in electrolytes. Conductivities change only briefly, for the capacity of the masses of water in the Amazon to withstand dilution is very great. Thus conductivity, pH and temperature fluctuate within narrow limits.

The heavy load of inorganic solids which is kept in suspension at higher current speeds may be used by the vegetation as a supplementary source of nutrients, for their root masses entrap many times their own weight of these solids. The quantity of root tissue formed by *Paspalum repens* under these conditions is only one-third as great as the quantity formed by plants in biotopes without this supply of suspended materials (JUNK 1970).

Autochthonous stands of floating vegetation normally do not last longer than eight months, because of the large fluctuations in water levels and the associated current action. During low water levels from October to January, there is usually no autochthonous floating vegetation on the banks of the Amazon. Since there is relatively little time for development, the fast-growing forms *Paspalum repens* and *Echinochloa polystachya* are most often dominant. Less important are *Hymenachne amplexicaulis, Oryza perennis* and *Panicum chloroticum*[1]. *Eichhornia, Pistia, Salvinia* etc. occur, but are of no importance, for they do not form cohesive stands and are therefore easily washed away by the currents. *Leersia hexandra* and species of Cyperaceae were not found in this biotope.

The fauna, too, is primarily influenced by currents and the large amounts of inorganic suspended matter. With increasing current speeds, and consequently increasing loads of suspended solids, faunal abundance decreases. Stronger currents also exert a direct effect, in that they can wash away non-sessile animals. The large amounts of inorganic material in relation to organic material suspended in the water hinders the feeding activities of filter feeders. Probably for these reasons, Conchostraca do not normally occur in this biotope. In general, the proportion of Crustacea in the fauna increases, but that of Insecta decreases, as current speeds decrease.

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[1] *Paspalum fasciculatum* normally does not contribute to the structure of the 'Whitewater Type', since it is submerged during high water. This is why it was left off the list, in spite of its wide distribution in the várzea region.

Faunal abundance increases strongly from the periphery of the stands, inward. Only the numbers of Trichoptera, Ephemeroptera and Hemiptera remain constant through this transition, or even decrease slightly. Total abundance can be as high as 100 000/m^2 in the central zone under favorable circumstances, but it is normally around 50 000/m^2 or less. No major fluctuations or changes of any duration in the abundances of different faunal groups were evident. Should any such fluctuations occur, they would probably be obscured to a large degree by the effects of current and suspended solids.[1] Variations which were observed within the separate populations were mostly due to local causes, and had no significance over the region as a whole.

Like abundance, biomass is dependent on current speed and the amount of inorganic suspended matter. Dry weights varied from 0.3 g/m^2 in locations exposed to the current to 4.2 g/m^2 in especially well-protected places in the inner parts of the stands. When a separate conversion factor is used for mollusks, these values are equivalent to a range in wet weights of 1.5 to 20 g/m^2. In the 'Whitewater Type' of floating vegetation, animals in the larger size classes which were picked out prior to the subsampling procedure were rare. Therefore, the weights of such animals from all stations of this biotopic type were summed and averaged over the total number of samples. This yielded a mean dry weight of 0.208 g/m^2 in the whitewater biotope. This amount has been included in the figures stated earlier in this paragraph.

b) 'Lago Type A'

The combination of factors which determines the structures of the Whitewater Type, current and the associated amount of suspended solids, did not occur in the várzea lakes. While some currents (e.g. Lago Manacapurú) and high turbidities (e.g. Lago do Xiborena at low water) were observed, the two factors were not interrelated. In the Solimões-Amazon, high turbidity results from the current and is dependent on it, but in the lakes, inorganic turbidity is mostly due to wind-induced turbulence which stirs up the finer sediments from the bottom. These are lentic waters, and phytoplankton production is possible even in the presence of high turbidity. Normally, however, there is essentially no current and the amount of inorganic suspended solids is very low.

Water in these lakes is diluted over the course of the year by drainage of electrolyte-poor water from the terra firme and by rainwater. Electrolyte concentrations and pH can undergo considerable annual fluctuations.

These changes can be so great as to have striking effects on the fauna in the floating vegetation. This was clearest in Lago Manacapurú, where conductivity fell below 10 μS_{20} and total abundance was less than 50 000/m^2. However, results from several stations including

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[1] MARLIER (1965) describes an annual cycle for the Ephemeroptera.

the one in Lago dos Passarinhos showed that no observable effect occurred at 30 μS_{20}. Conductivity must obviously be extremely low before it has any such limiting effect, direct or indirect, on general faunal abundance.

It should be pointed out, however, that elctrolyte concentrations alone give no indication of the amount of plant nutrients, which are present. The várzea lake does not have a true hypolimnion because of its shallowness, and remineralization proceeds rapidly at the high ambient temperatures. Nevertheless, when the weather remains calm and conditions are favorable for longer periods, thermal stratification can be formed. As a result, considerable quantities of plant nutrients are cut off from the upper water layers. MARLIER (1965) using his measurements of oxygen concentrations, asserts that complete overturn of these lakes occurs only at low water. Such temporary depletion effects the growth of sessile and planktonic algae. Experiments in Lago Calado with excelsior, an artificial substratum, have shown that these, in turn, are of great importance to the fauna.

In flowing whitewater, the roots of *Paspalum repens* entrap large amounts of inorganic solids, but these are not available in the sedimented water of the lakes. Instead, the root matrix fills mainly with voluminous organic detritus, phytoplankton and $Fe(OH)_3$. Development of the roots is about three times as great as in flowing whitewater (JUNK 1970). The stands of plants generally reach a greater age in the lakes where the danger of fragmentation or of being washed away by the current is much less. Because the root development is greater, these stands are also more dense. Weak 'secondary colonization' by non-floating plants can begin.

Wherever the lakes are continuously connected with the main river, water levels undergo wide annual fluctuations which decimate the floating vegetation. Even so, both *Paspalum repens* in lentic waters and *Echinochloa polystachya* can develop signs of senescence before the stands fall dry. This is due to a steadily decreasing ratio of the mass of tissue capable of photosynthesis to the total plant mass. This is expressed as the ratio of vegetative tips to total rhizome mass. The result is a steep decline in the rate of growth and, for *Paspalum repens* , the formation of thin, hard shoots which grow perpendicularly from the internodes and build their own root network. Sometimes, very strong local decomposition sets in after only eight months, so that the stands reach an age of only one year and a maximum density of about 6 - 8 metric tons of dry weight per hectare. Decomposition is augmented by the high temperatures (sometimes over 40°C) which are produced by solar radiation in the unshaded central zones of older stands (JUNK 1970).

Oxygen depletion can occur because exchange of water within the plant mass is restricted; but does not proceed to the points of anoxia or hydrogen sulfide formation. Still oxygen tensions can fall low enough beneath a thick plant cover, especially in older stands and during calm weather, to become limiting for many species of fishes. Under these conditions, the vegetation can have a detrimental influence on the fish crops.

The number of individuals per m^2 is normally much higher in this biotope that the former one. Usually, abundances are between 100 000 and 300 000/m^2. Numbers of less than 50 000/m^2 occurred, however, during temporarily very low electrolyte concentrations in Lago Manacapurú. The highest, over 700 000/m^2, also occurred in Lago Manacapurú. Usually, faunal densities are about the same in the peripheral and central zones of the stands, or decrease by about one-third toward the center. Conchostraca are regularly present in all parts of the stands, and are often extremely abundant. Ephemeroptera, Trichoptera and Hemiptera prefer the peripheral zone and are absent or rare in the central portions. In contrast, Ostracoda attain higher densities in the central zones of the stands.

On the whole, there were no strongly dominant and easily generalized factors in the lakes which could compare to current and the amount of suspended solids in the first biotope. As a result, considerable fluctuations in faunal abundance occurred during the course of the year which were attributable to local factors; for example, available nutrients, biotopic conditions for the adults of aquatic insects, etc. Indeed, these variations are so locally restricted that considerable differences in the abundance and composition of the aquatic fauna could coexist in different parts of the same lake. Lago Calado, for instance, had a faunal pattern near its outlet which was very different from that in its inlet. In Lago Manacapurú, there were enormous maxima in faunal abundance just before the stands fell dry in 1967 and 1968. Copepoda were largely responsible for the maximum in 1967, and Diptera were scarcely found at all; but in 1968, the maximum was spread over many faunal groups, and included large numbers of Diptera.

Biomasses varied between 2.5 and 11.6 g dry weight per m^2. When Mollusca are calculated separately with an appropriate conversion factor, an estimated equivalent range of 12 - 62 g wet weight per m^2 is obtained. The abundance of animals in the larger, presorted size class was much greater at all stations than in the whitewater biotope. The average weight of these animals for all stations in the Lago Type A was used in calculating total biomasses, to avoid extremes due to chance which did not correspond to natural conditions. This overall mean was 2.22 g dry weight per m^2; it has been included in the biomass data given above.

In October 1963, MARLIER (1965) determined the faunal biomass in three samples from floating vegetation in Lago Redondo, a várzea lake on Careiro Island near Manaus. He reports the following figures:

13.904 g	dry weight per m^2	(39.68 g wet weight)
10.545 g	"	(39.36 g ")
3.924 g	"	(18.944 g ")

The smaller, motile forms were not included in this figure. The high dry weights in the first two samples, according to MARLIER, were largely due to a high proportion of mollusca. His values are of the same general magnitude as ours.

In summary, it may be said that the Lago Type A biotope is the richest in abundance and the most productive but it is also the one with the greatest local quantitative and qualitative heterogeneity.

c) 'Lago Type B'

In these lakes there is no current at all, so there is no danger that the stands will be disrupted. Thus slower-growing plants such as *Leersia hexandra* and various floating species of the family Cyperaceae can also form larger, continuous mats. Moreover, these plants decompose more slowly than, for example, *Paspalum repens*, and under suitable conditions they can accumulate into hummocks of several years' growth. The water content of the rhizomes of *Leersia hexandra* is significantly less than in those of *Paspalum repens* or *Echinochloa polystachya* (JUNK 1970). This may be the reason they are less susceptible to decomposition. Clearly, there is some minimum quantity of moisture during the dry season which will support the development of larger mats of *Leersia hexandra* and floating species of Cyperaceae. In time, such hummocks attain considerable thickness, but never become as thick as the true floating islands. The monospecific nature of these stands leads to an equilibrium between growth and decomposition after a short time, unlike the stands which are heavily overgrown with a mixture of 'secondary colonizers'. In Lago dos Passarinhos we found a maximum of six layers of dead rhizomes and roots in a pure stand of *Leersia hexandra*. This is equivalent to a dry weight of 25 metric tons per hectare. The system cannot become much thicker, for nothing but the roots holds the horizontally deposited layers together. As soon as the roots decompose, the lowermost layers drop to the bottom of the lake in chunks.

A strong secondary colonization by non-aquatic plants has the effect of making the floating material denser and less homogeneous as leaves and branches collect on it. Plants with stronger roots bind the layers together more effectively, so that floating islands over 1 m thick and of a consistency similar to peat can be formed. These islands, to judge from the quantity of accumulated vegetation, must be at least 20 - 30 years old in many cases, and can reach much greater ages (Lago Parú). Even in the younger and less dense stands, exchange of water with the surrounding open areas is severely impeded. Total anoxia frequently occurs in the inner portions of such stands, and H_2S can be formed. The older, denser floating islands are totally devoid of dissolved oxygen, except for a narrow zone around the periphery.

In the peripheral zone, faunal abundance is about the same as in stands of Lago Type A. Farther inward, numbers decrease rapidly in younger stands. Ephemeroptera, Trichoptera and Conchostraca generally drop out altogether. Although numbers of Ostracoda also decrease strongly, they are the dominant faunal group (Lago dos Passarinhos). In older stands with more secondary colonization and denser structure, abundance is very low only a few meters (in extreme cases, only a few decimeters) from the outer edge. It is so low, in fact, that the central zones of these islands can be considered totally lacking in animals of the taxa studied here.

Like numbers of individuals, the biomasses of the faunal groups studied here were also much less in this biotope. In a pure stand of *Leersia hexandra* in Lago dos Passarinhos, biomasses were between 0.16 and 0.29 g dry weight per m^2. This is equivalent to a range of wet weights from about 1.0 to 1.8 g/m^2. No larger specimens of the groups Decapoda, Odonata, Mollusca, etc. comparable to those in the other two biotopes were found. Biomasses of the faunal groups included in these investigations were zero in the thick floating islands in Lago Parú and Lago Castanho.

We feel justified in raising these perennial hummocks to the rank of a distinct biotope because they differ not only in degree, but also in kind from the less thick, annual (at the oldest) stands. Although the two can arise side by side under identical aquatic conditions. the factors which affect the fauna which develop in them are of fundamentally different origins. In the more open annual stands, factors of the local surroundings exert a dominant influence on the flora and fauna. Oxygen curves show that exchange of water in the stands with the surroundings is still relatively free. At this level, the peripheral zone of the perennial stands is quite comparable to the Lago Type A. In the inner portions of the stands, the importance of factors in the surrounding milieu declines markedly. The extremely thick floating islands utilize the lakes mainly as a medium which keeps them constantly wet. In their central zones, they constitute a system which has its own set of controlling factors, and is essentially independent in many respects (e. g., dissolved gasses and nutrients) of the surrounding body of water.

The subdivision of floating vegetation into three biotopes as laid forth in the preceding section is based on major ecological differences. The effects of the distinguishing factors on the faunal communities have been studied mainly with regard to abundance because, with the exception of Conchostraca, it has not been feasible to separate the fauna farther than to higher taxonomic groups, each with many species. Since even closely related species often have very different biotopic requirements, it is very probable that the species compositions of communities in different biotopes will also be very different. Perhaps more detailed autecological studies of the fauna will lead to a more highly differentiated subdivision of the kinds of stands. The present system for biotopes of floating vegetation presented here enables rapid classification of stands on the basis of a few characteristic criteria. This classification provides conclusive information about faunal abundance and biomass, and at least in its major trends, about the composition of the fauna.

2. Influence of water level fluctuations on the fauna

Samples taken at different times of year and different water levels show that faunal abundance does not decrease in many cases, even up to the time just before the stands fall dry. Although some of the animals have dormant, dessication-resistant phases, e.g., Cladocera and Bryozoa, such phases occur throughout the year. No accumulation of these phases could be found just before the stands dried out. Therefore, the annual drying of the stands must be a catastrophe for the fauna, insofar as they are unable to seek out alternative habitats (as, for example, flying insects). Perhaps this can be better comprehended when we realize that the yearly cycle of high and low water levels does not have the same incisive effect on all bodies of water in the várzea region. On one hand, the amplitude of water levels varies from year to year, and on the other, even the lowest water levels leave behind sufficient suitable biotopes in residual and isolated lakes to insure recolonization when water levels rise again. The constancy of water temperatures obscures much of the difference between dry season and rainy season for the aquatic fauna. Moreover, local rainfall, a factor to which the animals might be able to react, is not the most important factor in local water levels. This is shown by comparison of water levels with precipitation records (fig. 32). Rather, water levels are determined by rainfall far away in the catchment areas of the large tributaries, and by melting snow in the Andes, where hydrographic and climatic conditions are very different from those in the Amazonian lowlands. Thus the life cycles of aquatic animals in the várzea region are more strongly influenced by local than by regional factors. Fluctuations which might occur in some species over larger areas and on a longer time-scale are strongly suppressed by the local environment. There is no seasonal rhythm of the sort which is so common in the temperate zones.

3. Comparisons with similar biotopes in tropical waters outside the Amazonian region.

It requires no elaboration to state that a comparison of tropical and non-tropical areas is very problematic. Metabolic processes are very different because of continually high temperatures. Therefore, only tropical regions will be compared with our investigations.

Only PETR (1968) has conducted quantitative investigations of the fauna in biotopes which are comparable to the ‘floating meadows’ of the Amazonian várzea. His results pertain to the aquatic animals in stands of *Pistia stratiotes* and *Ceratophyllum demersum* in the Volta Reservoir in Ghana. Comparison with the fauna in *Ceratophyllum demersum* stands cannot be made, since his results are expressed as numbers of individuals and biomasses per unit dry weight of plant tissue. His results from *Pistia stratiotes* stands, however, are expressed on a square-meter basis, so comparison is possible.

He cites abundances between 5 000 and 15 000/m^2. These values are far below those for *Paspalum repens* stands in the várzea lakes which are most biotopically similar to the conditions in the Volta Reservoir. It should be mentioned, however, that PETR does not consider his results to be quantitative for some very abundant groups, such as Copepoda and Cladocera, due to the sometimes very small size of the individuals. The same qualification must be applied to a comparison of his biomasses with those from várzea lakes. PETR reports formalin-wet weights of 5 to 35 g/m^2. These values, too, are lower than the calculated wet-weight biomasses for várzea lakes.

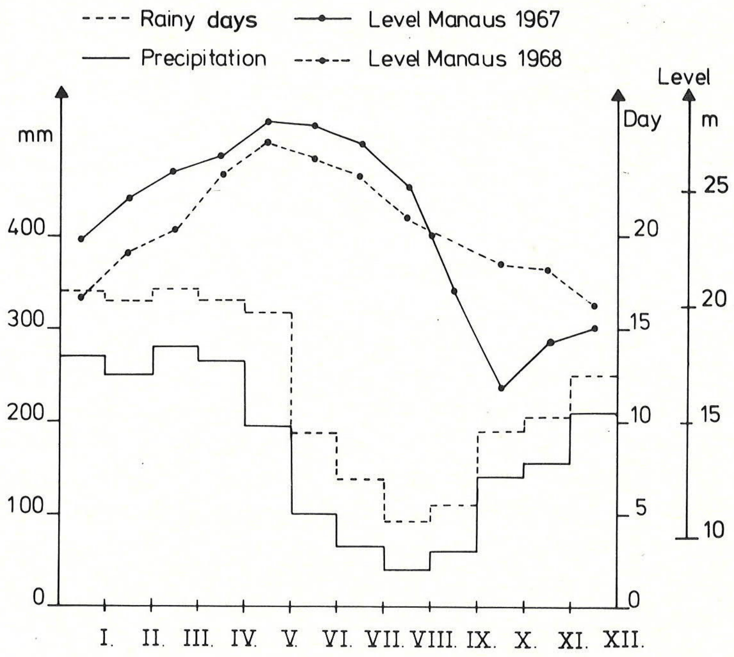

Fig.32: Comparison of water level from 1967 and 1968 with the average precipitation and the number of rainy days in Manaus.

A more detailed discussion of PETR's results in regard to differences within separate faunal groups does not seem useful at this time. The Volta Reservoir is a man-made lake of enormous area, and had been in existence only 10 months when those studies were made. Its aquatic fauna was not yet at a level of development comparable to natural waters of similar type.

In closing, it should be pointed out that the 'floating meadows' are of very great importance with respect to primary production, as well as secondary production, in the várzea waters. In flowing whitewater, autochthonous phytoplankton production is very small, if it exists at all, so the 'floating meadows' are by far the most significant site of primary production in this biotope. Of course, these stands are clearly not closed systems. Thus they may be utilized heavily (e. g., as cattle silage) without fear of disturbing their metabolism or the natural systemic equilibrium. The enormous water masses of the Amazon continually renew the supply of nutrients to these systems.

The best proof of this lies in the fact that high water levels regularly disrupt and wash away these plants in a natural seasonal rhythm. They are completely removed from the system, then fully replaced by new growth.

The zone of floating plants around the edges of várzea lakes, which generally have clear water and autochthonous phytoplankton production, nevertheless contributes significantly to primary production. Since the water in these lakes is renewed annually by fluctuating water levels, this biomass can also be intensively utilized.

The numbers of individuals per m^2 which we have found in the floating vegetation are very high relative to other biotopes, e.g., that of the lake bottom. BRAUN (1952) reports a maximum of 12 000 benthic animals/m^2 in Lago Jurucui, a lake in the mouth region of the Tapajós. We found a maximum of 786 500/m^2 in the 'floating meadows'. According to MARLIER (1965), the biomass of the fauna in 'floating meadows' was 49 times as great as that of the benthic fauna in Lago Redondo.

Thus the floating vegetation represents a biotope which, with few exceptions, offers very good living conditions for aquatic animals. It is so heavily populated that it must be one of, if not the richest of biotopes in the water bodies of the várzea, both in total faunal abundance and in the number of species.

Summary

Besides their importance for primary production, (JUNK 1970) the floating vegetation in the varzea region of the Amazon must be taken into consideration as a very important factor for the secondary production in the waters of this region as well. The floating stands represent a biotope which, with few exceptions, offers very good living conditions for aquatic animals. Accordingly they are populated with a large number of individuals and species. The maximum values found using a net of mesh size 223 microns were 780 000 individuals per m^2 which is equal to 11.6 g dry weight /m^2 (62 g fresh weight).

The plants are used by the animals as a substratum and partly for nutrition. Experiments with excelsior as a substratum have shown that phytoplankton and detritus, trapped in the roots, are very important for nutrition for the population. High quantities of inorganic suspended material in combination with current (flowing white water) strongly reduce the number of individuals especially the filtering forms. Under such conditions, *Cyclestheria hislopi* BAIRD (Fam. Conchostraca) was not found.

In dense floating islands, which are several years old, the oxygen content can be the limiting factor for the population of aquatic animals. In general we can say that the development of the aquatic fauna is influenced more by local than by regional factors.

Because of the complex composition of the fauna it can be shown that the short term variations of the ecological factors are shown better by the number of individuals than by the biomass. Animals with a fast succession of generations react to changes in the ecological conditions, and have a greater influence on the number rather than the biomass. of individuals, due to their small size.

From the point of view of the colonization by aquatic invertebrate fauna the floating vegetation could be divided into three different types, which are briefly characterized in Table 12. The factor which lead to this division and their effects on the animals have been investigated and discussed extensively.

For further clarification of the relationship between fauna and substratum, experiments have been conducted with an artificial substratum, excelsior.

Table 12: Characterization of the floating vegetation with respect to its faunal inhabitants.

"White water Type"	"Lago Type A"	"Lago Type B"
Arises only in flowing whitewater rich in suspended solids (e.g. the Amazon)	Arises in primarily "sedimentated" standing waters	Arises only in standing waters
Material entrapped by the roots is predominantly inorganic suspended matter	The roots entrap primarily organic suspended matter and $Fe(OH)_3$	The roots entrap primarily organic suspended matter
The water has low transparency	The water normally has high transparency	The water normally has high transparency
Only small variations in pH or conductivity	pH and conductivity fluctuate through the year	pH and conductivity fluctuate through the year
The vegetation consists mostly of *Paspalum repens* and *Echinochloa polystachya*	The vegetation consists mostly of *Paspalum repens* and *Echinochloa polystachya*	The vegetation in early stages consists predominantly of *Leersia hexandra* and species of the family Cyperaceae
Normally exists only from February until November	Normally persists for a maximum of one year	Stands are perennial
Low stand density (more open growth pattern)	Low or high stand density (open or denser growth pattern)	Stand density high to very high
Usually no "secondary colonization" by terrestrial plants	Weak "secondary colonization" by terrestrial plants	In some instances extremely heavy "secondary colonization" by terrestrial vegetation
Moderate root development by *Paspalum repens*	Strong root development by *Paspalum repens*	— — —
Homogeneously favorable O_2 conditions	Very good to moderately good O_2 conditions	Central zones of the stands more or less anoxic, H_2S present
Total faunal abundance as high as 100.000 individuals per m^2	Total faunal abundance up to about 780.000 individuals per m^2	Animals rare or totally absent in the central zones
Conchostraca normally lacking	Conchostraca are regularly present, and sometimes extremely abundant	Conchostraca are present only in the peripheral zones
Biomass 0.3 - 4.2 g dry weight/m^2 (1.5 - 20 g/m^2 wet weight)	Biomass 2.5 - 11.6 g dry weight/m^2 (12 - 62 g wet weight/m^2)	Biomass 0 - 0.3 g dry weight/m^2 (0 - 1.8 g wet weight/m^2)

Resumo

Além da sua importânica para a produção primária (JUNK 1970) a vegetação flutuante na região de várzea do Amazonas deve ser considerada importante também para a produção secundária nos corpos d'água da região. A vegetação flutuante representa com poucas exceções um biótopo ótimo para a fauna aquática. Em correspondência é povoada por um grande número de espécies e indivíduos. Como valôres máximos foram verificados 700 000 indivíduos/m^2 respectivamente 11.6 g de pêso sêco/m^2 = 62 g de pêso fresco (abertura das malhas 223 micra).

As plantas servem à fauna colonizadora como substrato e parcialmente também como base nutrutiva. Como experiências com raspas de carpintaria m/usadas como substrato mostraram, també fitoplâncton e detrito introduzidos nas raízes são importantes como alimento em especial para as formas filtradoras. Com quantidades maiores de sedimentos inorgânicos suspensos em combinação com correnteza fraca a colonização, especialmente dos filtradores, regride. Sob estas condições não se verifica a presença de *Cyclestheria hislopi* BAIRD (Fam. Conchostraca).

Em ilhas de vegetação com vários anos de idade o teor de O_2 pode-se tornar um fator limitante para o povoamento. De maneira geral pode ser dito que o desenvolvimento da fauna aquática é influenciado mais por fatôres regionais do que supraregionais.

Com base na composição complexa da fauna verificou-se que oscilações dos fatôres ecológicos a curto prazo são melhor visíveis mais no número de indivíduos do que na biomassa, uma vez que as formas com seqüência de gerações mais rápida, que melhor se adaptam ás variações do ambiente, influenciam antes o número de indivíduos devido ao seu pequeno tamanho, do que a biomassa.

Sob o aspecto da colonização com fauna de invertebrados aquáticos, a vegetação flutuante é subdividida em três tipos distintos, e os fatôres que os condicionam são analisados na tabela 12. Os fatôres que levam a esta divisão e os seus efeitos sôbre os animais foram investigados e discutidos extensivamente.

Para uma maior elucidação das relações entre fauna e substrato foram feitas experiências com substrato artificial, raspas de carpintaria.

Tabela 12: Caracterização da vegetação flutuante com relação a seus habitantes animais.

"Tipo de água branca"	"Tipo de lago A"	"Tipo de lago B"
Biótopo da água branca corrente rica em suspensóides	Biótopo da água branca sedimentada do tipo A	Biótopo da água branca sedimentada do tipo B
Origina-se apenas em água branca corrente rica em suspensóides	Origina-se preponderantemente em água sedimentada estagnada	Origina-se apenas em água estagnada
Entre as raízes são retidos principalmente suspensóides inorgânicos	Entre as raízes são retidos principalmente suspensóides e $Fe(OH)_3$	Entre as raízes são retidos principalmente suspensóides orgânicos
A água tem visibilidade pouco profunda	A água tem via de regra visibilidade muito profunda	A água tem via de regra visibilidade muito profunda
Sem oscilações significativas de pH e condutibilidade elétrica	Oscilações de pH e condutibilidade elétrica ocorrem durante o ano	Oscilações de pH e condutibilidade elétrica ocorrem durante o ano
A vegetação consiste principalmente em *Paspalum repens* e *Echinochloa polystachya*	A vegetação consiste principalmente em *Paspalum repens* e *Echinochloa polystachya*	A vegetação consiste de início preponderantemente em *Leersia hexandra* e espécies da família Cyperaceae
Existe normalmente de fevereiro a novembro	Persiste normalmente no máximo durante um ano	Perene
Forma de crescimento sôlta	Forma de crescimento de sôlta a densa	Forma de crescimento de sôlta a extremamente densa
Normalmente sem "povoamento secundário" de vegetação terrestre	Fraco "povoamento secundário" de vegetação terrestre	Parcialmente com "povoamento secundário" de vegetação terrestre extremamente intenso
Reduzido desenvolvimento radicular de *Paspalum repens*	Intenso desenvolvimento radicular de *Paspalum repens*	—
Condições de O_2 uniformemente boas	Condições de O_2 de muito boas a fracas	Na zona central ± livre de O_2, ocorrência de H_2S
Povoamento animal até ca. de 100 000 indivíduos/m^2	Povoamento animal até ca. de 700 000 indivíduos/m^2	Na zona central com fraco ou sem povoamento
Normalmente sem Conchostraca	Regularmente com Conchostraca, frequentemente com desenvolvimento de massas	Conchostraca só na zona marginal
Biomassa de 0.3 - 4.2 g/m^2 em pêso sêco (1.5 - 20 g/m^2 em pêso frêsco)	Biomassa de 2.5 - 11.6 g/m^2 em pêso sêco (12 - 62 g/m^2 em pêso frêsco)	Biomassa de 0 - 0.3 g/m^2 em pêso sêco (0 - 1.8 g/m^2 em pêso frêsco)

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